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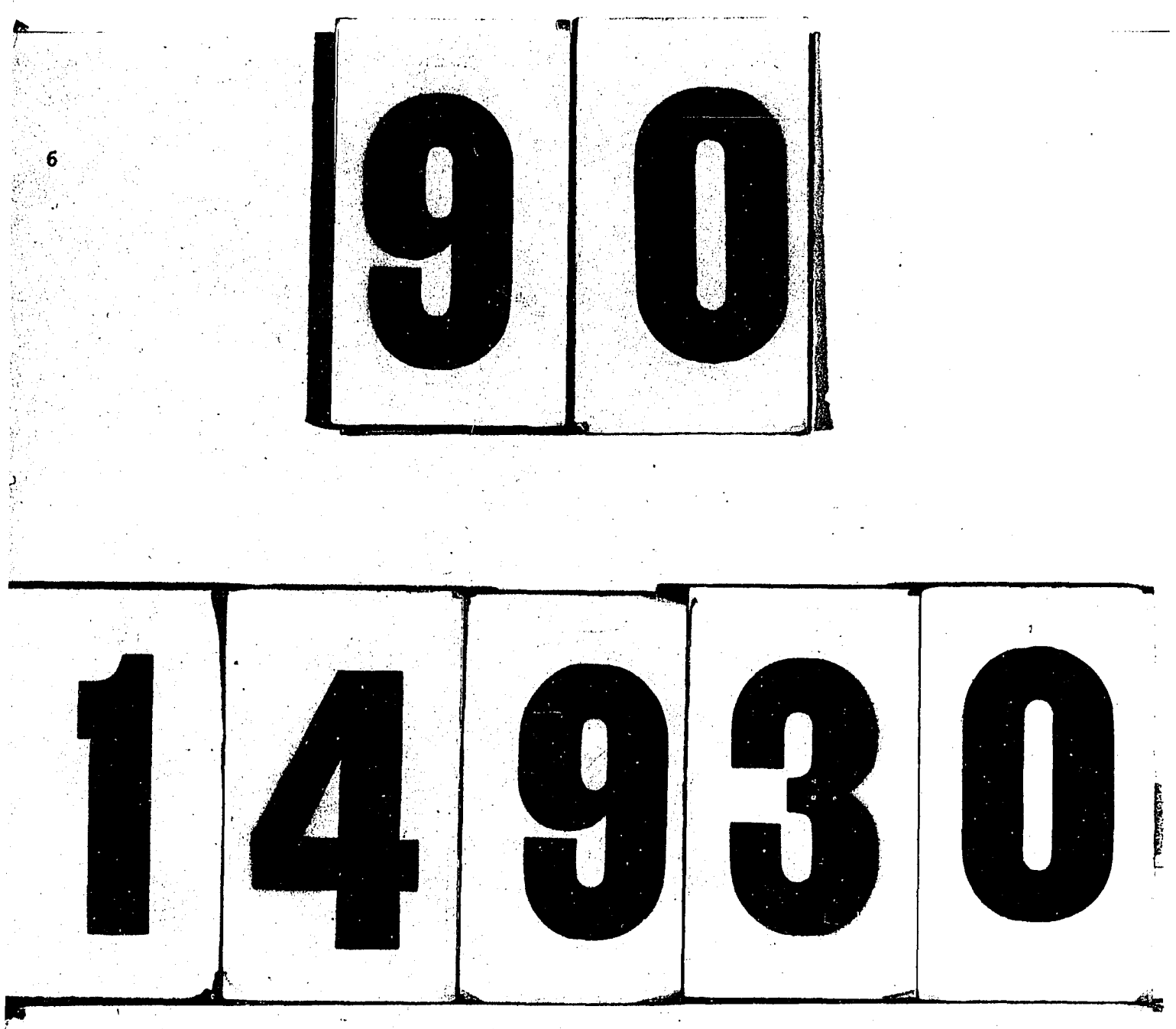

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Estimates of quantitative genetic parameters in IAP2B random-mating sorghum population

by

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DEDICATION

In memory of my Dad

September 1, 1989

INTRODUCTION

Improvement of plant species for specific characters is a goal of all plant breeders. Recurrent selection has been used to increase the frequency of favorable alleles for both qualitatively and quantitatively inherited traits. When additive gene action plays a major role in the heredity of a trait, improvement of populations *per se* also should improve the performance and general combining ability of inbred lines developed from those populations.

The incorporation of genetic male sterility into sorghum [*Sorghum bicolor* (L.) Moench] germplasm has provided a means for making large-scale cross pollinations. With the use of genetic male sterility, random-mating populations were constructed and many were characterized for quantitative genetic parameters (Doggett, 1988). Additive genetic variance was found to be a large component of the total genetic variance for most traits examined. Phenotypic recurrent selection has been used to take advantage of additive genetic variance and numerous improvements in sorghum random-mating populations have been reported (Ross and Gardner, 1983).

Development of IAP2B random-mating sorghum population was initiated at the Iowa Agriculture Experiment Station in 1977 (Atkins, 1982), and four cycles of gridded mass selection for individual panicle grain weight were conducted. Objectives of the experiments reported in this dissertation were: (1) to characterize and evaluate the breeding potential of IPA2B population *per se* and (2) to examine the changes that occurred in plant characters from the initial cycle (C0) through the

fourth (C4) cycle. Data were obtained for grain yield, components of yield, plant height, and days to midbloom in two experiments grown near Ames, Iowa during 1984-1988. Experiment I examined trends and means, and estimated inbreeding depression among S_1 and half-sib composites over four cycles of selection. In Experiment II, population means, variances, and heritabilities were estimated for S_1 families selected from the initial and fourth cycles. Phenotypic and genotypic correlations among characters also were calculated for S_1 families from the two cycles, and estimates of expected gain and correlated responses to selection were determined.

LITERATURE REVIEW

Historical Perspective

Sorghum (Sorghum bicolor L. Moench) is a naturally self-pollinated species. Early sorghum breeding efforts focused on the improvement of pure-line varieties. The successful use of hybrid varieties in corn (Zea mays) prompted sorghum breeders to investigate the potential advantages that hybrids might offer in sorghum. Subsequent research (Karper and Quinby, 1937; Bartel, 1949; Stephens and Quinby, 1952) indicated that hybrid vigor was expressed in sorghum crosses. Karper and Quinby (1937) reported that F_1 hybrids outyielded (total plant weight) the mean of their parents by as much as 300%. The commercial production of hybrid sorghum seed, however, awaited the development of an economically feasible method of cross pollination on a field scale.

A male-sterile plant was found in a field of Texas Blackhull Kafir by Stephens in 1937. Inheritance studies revealed that a pair of homozygous-recessive alleles (later designated $\underline{ms}_2$ $\underline{ms}_2$ by Stephens and Quinby, 1952) were responsible for pollen sterility in that plant. Stephens (1937) proposed a crossing scheme for producing hybrid sorghum seed that utilized the $\underline{ms}_2$ male-sterility system. The method was never used commercially because roguing of fertile plants in one seed-production block would be necessary.

Another male-sterile plant, found originally in a field of Day milo, was reported by Stephens et al. (1952). Their results also indicated that the male sterility was controlled by genetic factors. The unique feature

of their system was that fertility of the progeny produced by using Day milo as the female parent was dependent upon what line was used as the male parent. The authors proposed a method to produce three-way hybrids by using their male-sterility system, but it was not used appreciably for commercial seed production.

Stephens and Holland (1954) continued the research started by Stephens et al. (1952). Data from segregating generations of some of their materials revealed a male sterility in sorghum that was controlled by a cytoplasmic-genetic male-sterility system (cms). Their studies showed that plants that possessed the Milo cytoplasm, in combination with recessive alleles of the Kafir genome, were male-sterile. Quinby and Martin (1954) outlined a scheme for producing hybrid grain sorghum by using the cms system. The scheme provided an efficient and economically feasible method for commercial hybrid seed production.

The transition from pure-line varieties to F_1 hybrids in sorghum production was swift and nearly complete following Stephens and Holland's publication of the discovery of cms in 1954. By 1957, it was estimated that 15% of the total sorghum acreage in the United States was planted with hybrid varieties. One year later, the use of hybrids had increased to an estimated 50% of the total sorghum acreage (Duvick, 1959). Within ten years, nearly all of the grain sorghums grown were hybrids. Harvey (1977) found that 97% of the hybrid seed was produced by using the Milo cytoplasm-Kafir genome system. That system, however, limited genetic diversity among hybrids by imposing restrictions on parental combinations. Harvey (1977) noted (in a survey of the grain sorghum germplasm base in

the United States) that private seed companies used only 35 public inbreds in hybrid seed production. These inbreds made up 87% of the female parents and 69% of the male parents that were being used by the companies in hybrid seed production. Expanded and better utilization of the elite germplasm base used for inbred line development was needed to ensure continued improvement of future hybrid varieties.

Quantitatively inherited traits, such as grain yield, are controlled by many genes, each conveying a small effect in relation to phenotypic expression of the trait. A large number of favorable alleles and allele combinations differ among elite inbred genomes. These favorable DNA segments need to be reassembled and restructured to form the best combinations, and then be incorporated into a single genotype. Recombination is necessary to accomplish that process. The problem facing plant breeders is the fact that the population size required to isolate individual genotypes with a majority of favorable DNA segments exceeds the resources of breeding programs (Bailey and Comstock, 1976; Bailey, 1977; Sneep, 1977; Yonezawa and Yamagata, 1978). Recurrent selection offers a breeding scheme that substitutes time for large population size.

Recurrent Selection

Fewer individuals are needed to maintain all favorable alleles in a population than would be necessary to obtain and identify one genotype with all favorable alleles present. Recurrent selection methods are designed to increase the frequency of favorable alleles in the population *per se*, thus improving the opportunity for extraction of superior inbreds

to be used in hybrid combinations.

Recurrent selection is a cyclical process of evaluation and recombination of selected genotypes that is used to improve random-mating populations. Hull (1945) first used the term "recurrent selection" to describe selection for general combining ability. However, breeding programs described previously by Hayes and Garber (1919) and Jenkins (1940) fulfilled the requirements established by Hull (1945) to be termed "recurrent selection". The basic objectives of recurrent selection are to shift the mean performance of the population in a favorable direction while maintaining genetic variability for the trait(s) of interest.

Recurrent selection can be conducted either within one population or between two populations. Moll and Stuber (1974) used the terms intrapopulation improvement and interpopulation improvement. Intrapopulation procedures maximize improvement of the individual populations per se and inbred lines developed from them. The units of selection can be individual genotypes, selfed families, half-sib families, or full-sib families. Interpopulation procedures maximize the improvement of population crosses and hybrids formed between lines developed from the populations under selection. The units of selection can be either half-sib or full-sib progenies of crosses between two populations.

In theory, if additive gene action is the predominant source of variation within a species, then improvement of the population per se also should improve inbred lines derived from the population (Falconer, 1981; Hallauer and Miranda, 1988). The improved inbred lines should exhibit

good general combining ability in hybrid combinations with other inbred lines. Studies with sorghum have demonstrated that additive genetic variance, or general combining aiblity, plays a major role in the expression of many agronomic traits (Kambal and Webster, 1965; Niehaus and Pickett, 1966; Voigt et al., 1966; Beil and Atkins, 1967; Liang, 1967; Atkins et al., 1968; Kirby and Atkins, 1968; Malm, 1968; Fanous et al., 1971; Patanothai and Atkins, 1974; Jan-orn et al., 1976; Eckebil et al., 1977; Laosuwan and Atkins, 1977, 1978; Ross, 1978; Bittinger et al., 1981; Prest et al., 1983; Ibrahim et al., 1985; Lothrup et al., 1985a). Intrapopulation recurrent selection schemes should be successful for improving broad-base random-mating sorghum populations and inbred lines developed from the populations.

Three stages are common in all recurrent selection strategies. One cycle of selection should include (1) development of selection units, (2) evaluation of the units, and (3) intermating superior units or the parents of superior selection units (Hallauer, 1987). Detailed descriptions of different recurrent selection techniques were given by Hallauer (1986, 1987) and Hallauer and Miranda (1988). Unique modifications of the process have been established for each crop species. Recurrent selection programs in predominantly self-pollinated species such as sorghums are limited in size by the number of cross pollinations needed. Incorporation of genetic male sterility into sorghum populations permits large numbers of cross pollinations to be made with relative ease.

Sorghum Random-Mating Populations

Several strategies can be used to incorporate genetic male sterility into sorghum populations. The desired genetic male-sterile gene could be backcrossed into parental lines, and the derived backcrosses would be intermated in a diallel fashion to initiate the base population (e.g., Nordquist et al., 1973). Another technique described by Ross (1973) involved crossing parental lines to male-sterile segregates of an existing population with a desirable male-sterile gene present. Ratios of introduced germplasm to genetic background from the existing population could be adjusted by using backcross procedures. Three genetic male-sterility systems ($\underline{ms}_3$, $\underline{ms}_7$, and $\underline{a1}$) have been used widely in random-mating sorghum populations (Ross et al., 1971).

Genetic male sterility has provided a mechanism for large-scale cross pollinations in sorghum. Cross pollinations allow chromosome reassembly among parental genotypes as well as restructuring of linear DNA segments by cross-over events during meiosis. Recombination has been shown to release variability that was hidden within linkage blocks (Dogget, 1972a). Breakage of repulsion-phase linkages is desired, but maintenance of coupling-phase linkages is advantageous during the selection process. The optimum level of recombination during recurrent selection has been reviewed and discussed thoroughly by Piper (1985). Conflicting hypotheses exist regarding the level of intermating desired to maximize gain from selection. Researchers agree, however, that recombination at some level is necessary for plant improvement.

Recombination is helpful to plant breeders only if ample variability exists for the traits under selection. Diverse parental germplasm has been assembled in common gene pools for different species. Favorable alleles from each parent should provide the genetic variability necessary for researchers to meet the objectives of their investigations. Objectives may be short or long term, and parents of the population are chosen on the basis of these objectives. A good example for the selection of breeding materials was proposed at the Sorghum Research Conference in Puerto Rico (Eberhart, 1970). Four population types were established. Type I populations would include only superior U.S. germplasm; Type II populations would incorporate worldwide germplasm collections; Type III populations would be created from agronomically elite genotypes that displayed resistance to specific diseases or insects; and Type IV populations would be derived from germplasm pools intended to provide genetic diversity for long-range goals.

Random-mating sorghum populations have been developed and the merits of recombination exploited in quest of the "perfect" genotype. Undoubtedly, the goal of obtaining that perfect genotype has not been realized, but moderate steps have been taken in a positive manner. Characterization of populations is an initial step that enables breeders to estimate breeding potential of the gene pool and to choose efficient methods for its improvement. Accurate estimates of quantitative genetic parameters are necessary for proper interpretation and choice of the methodology to be applied. Analysis of quantitative genetic data obtained from cross-pollinated populations requires that individuals or families are chosen

in sufficient numbers to accurately represent the population, and that the individuals or families are chosen randomly. Biases that lead to imprecise estimates of parameters are introduced when these conditions are not met.

Ross and Hookstra (1983) estimated quantitative genetic parameters by using variance analyses from samples of 200 S_1 families taken from the same base population (NP16BR) in three different years. Sampling was done in different years to determine the influence of different growing seasons and different personnel on choice of the families and their subsequent progeny performance. Means, variance components, heritabilities, and predicted gains from selection estimated by using data from S_1 progenies generally were similar for the three samples. The results indicated that parameters calculated from data in any of the years could be used for plant breeding purposes. The authors concluded that, although minor quantitative genetic differences among years existed, the differences should have little effect on the choice of suitable methods for population improvement or the derivation of inbred lines from the population.

Ross et al. (1976) compared quantitative characteristics estimated from five random-mating sorghum populations (NP1BR, NP2B, NP3R, NP5R, and NP7BR). Parameters were calculated from a sample of 200 or more half-sib families from each population. Two commercially grown F_1 hybrids (RS626 and RS671) were included in the experiments as checks. NP1BR and NP2B displayed little genetic variability for grain yield and yield components. Although NP1BR originally was broad based, rigorous selection for plant

height and earliness may have reduced genetic variability for yield. NP2B was constituted from only eight elite inbred parents. Low frequency of favorable alleles for grain yield very likely was responsible for the limited expected gain from selection in these populations. The antherless (al) male-sterility gene was used to facilitate crossing in NP7BR, but the ms_3 male-sterility gene was used in the other populations. Grain yield data for NP7BR were biased downward because of extremely low yielding panicles that were obtained from pollinated antherless male-sterile plants. NP7BR showed little genetic potential as a breeding population due to limited genetic variability and low yield. NP3R and NP5R exhibited high levels of genetic variability and yielded nearly as much as the check hybrids. The latter two populations showed great potential for improvement by using recurrent selection schemes.

Jan-orn et al. (1976) estimated quantitative genetic parameters in an extensive study that involved 196 half-sib, 196 full-sib, and 196 S_1 families randomly sampled from NP3R. Grain yield exhibited a 1.38:1 ratio of dominance genetic variance to additive genetic variance from the combined analysis over two environments. Inbreeding depression was reflected by grain yield trends that displayed full-sib family means greater than half-sib family means, which in turn were larger than S_1 family means. These factors indicated that dominant gene action played an active role in the expression of grain yield in NP3R. The authors concluded that frequencies of favorable genes in the population may be less than 0.5, and that recurrent selection methods should work well for the improvement of NP3R. Values of predicted response from selection

by using a 10% selection intensity projected that S_1 family testing offered the greatest potential for the improvement of grain yield.

The performance of NP3R, NP5R, and NP7BR sorghum populations was examined in detail by Eckebil et al. (1977). Means, variances, heritabilities, genetic correlations, and predicted responses to selection were calculated from 200 S_1 families sampled randomly from each population. NP3R was somewhat higher yielding than NP5R and NP7BR. However, the genetic variability of NP5R for grain yield was twice that of NP3R. NP7BR exhibited substantially less genetic variability for yield than the other populations. NP3R was composed entirely of lines adapted in the United States, but a high proportion of exotic germplasm was introduced into NP5R. Predicted gains from selection for NP5R were larger for all traits except grain protein, when compared to values predicted for NP3R and NP7BR. The authors felt that the higher estimates for NP5R were due to larger levels of genetic variability estimated for that population. They concluded that both NP3R and NP5R should be suitable for improvement by recurrent selection when yield is the main selection criterion.

Bittinger et al. (1981) evaluated 150 progenies that were developed by using a Design I mating system where each of 50 randomly chosen pollen parents were crossed to a different set of three random seed parents. The ratio of estimated dominance genetic variance to additive genetic variance was 1.24:1 for grain yield. Additive variance was the major component expressed for all other traits evaluated (i.e., ratios < 1:1). The authors concluded that reasonable genetic gain could be expected by using recurrent selection in the random-mated population. However,

predicted gains for grain yield may have been due in part to pleiotropic effects of major height and maturity genes.

Ibrahim et al. (1985) evaluated two S_2 or S_1-derived families from each of 118 S_0 plants from PP18 sorghum popultion. PP18 was developed from a composite of S_2 seed selected for food-grain quality traits (kernel size, vitreosity, and color) that were taken from several random-mating populations at Purdue University (Cantrell, 1981). Breeding potential was assessed from the data obtained and genetic parameters were estimated subsequently for plant height, days to bloom, panicle compactness, panicle weight, kernel weight, lodging, weathering, kernel hardness, and vitreousness. Additive genetic variance components were significant for all traits. High estimates of predicted gain for most traits led the researchers to conclude that both recurrent selection and early-generation testing should be effective in PP18. They commented further that S_1-derived family selection should be superior to S_0-derived family selection for improvement of the traits measured.

A major objective of population improvement involves the extraction of parental material to be used as inbred lines that will produce superior hybrid varieties. In theory, if additive gene action plays a major role in gene expression for the traits of interest, then improvement of the population *per se* should improve inbred lines derived from the population. Briggs and Knowles (1967) stated that recurrent selection had not completely proven itself and that the ultimate proof awaited identification of successful hybrid combinations that originated from inbred lines derived from random-mating populations.

Otte et al. (1984) evaluated 60 F_1 sorghum hybrids developed by crossing two A-lines with 30 R-lines. The 30 R-lines consisted of three sets: set one was composed of ten well-adapted component lines from NP3R, set two contained ten lines selected from NP3R in Nebraska, and set three contained ten lines selected from NP3R in Arizona. The study compared the performance of hybrids involving the component inbred lines against hybrids that involved inbreds derived from the random-mating populations, on the basis of combining ability. Hybrids derived from male parents that were selected from NP3R significantly outyielded hybrids derived from component-line male parents. The authors stated that the results demonstrated that parental lines can be selected from a sorghum random-mating population that will produce suitable hybrids.

Most random-mating sorghum populations discussed to this point have had minimal, if any, intentionally directed selection applied between intermatings. Estimates of genetic parameters have been calculated by using data from families that were sampled randomly from each population. The results overwhelmingly suggest that recurrent selection procedures would be useful for improvement of agronomic characters in the populations *per se* and the inbred lines derived from the populations.

Phenotypic Recurrent Selection

The terms phenotypic recurrent selection and mass selection often are used interchangeably. However, marked differences can be delineated in implementation of the two procedures. Mass selection can be conducted with or without genetic recombination (Hallauer, 1987). Selection is

based on the phenotype of the individual organism without consideration of the performance of its progeny. Poehlman (1987) defined mass selection as "a system of breeding in which seeds from individuals selected on the basis of phenotype are composited and used to grow the next generation." Selection criteria are the same for mass selection and phenotypic recurrent selection, but recombination of selected individuals to form progeny for an improved population is an additional step required to meet the definition of phenotypic recurrent selection that is not required for mass selection. Intermating of selected individuals provides for the evolvement of new genic combinations that may not be present in the original population.

Phenotypic recurrent selection is the oldest and simplest form of recurrent selection (Nath, 1982; Ross and Gardner, 1983; Hallauer and Miranda, 1988). One cycle of selection can be accomplished with each growing season. Advantages of phenotypic recurrent selection can be realized when staff and funds are limited and only one crop per year can be grown (Doggett and Eberhart, 1968). Traits that exhibit relatively large genetic variance compared to nongenetic variance, i.e., those that display high heritability, are most effectively improved with this scheme.

Phenotypic recurrent selection has been used successfully for many highly heritable traits from a wide array of crop species. Law and Anderson (1940) reported significant increases for leafiness, number of culms, and basal culm diameter, and a significant decrease in plant height over five cycles of selection in big bluestem (Andropogon furcatus).

Eighteen cycles of phenotypic recurrent selection for increased vigor and disease and insect resistance have been successful in two populations of alfalfa (Medicago sativa) (Dudley et al., 1963; Hanson et al., 1972). Increased resistance was shown for common leaf spot, bacterial wilt, anthracnose, rust resistance, leafhopper, and spotted alfalfa aphid. Selection for early flowering was successful in Meadowfoam (Limnanthes alba) (Jain, 1979). Sprague and Brimhall (1950) increased oil content in corn by using phenotypic recurrent selection whereby seeds from self-pollination of selected ears were used to form the new population. That procedure allowed for control of both male and female parents in the selection process. Selection when both parents were controlled in pollinations was found to be successful by Bennett (1959) for hard seededness in crimson clover (Trifolium incarnatum) and by Graham et al. (1954) for resistance to common leafspot in alfalfa.

A comprehensive review of phenotypic recurrent selection from the maize literature was presented by Hallauer and Miranda (1988). Improvement of qualitative characters has been effective in most studies reported. Selection in maize has been effective for ear length (Hallauer, 1968; Cortez-Mendoza and Hallauer, 1979), ear height (Acosta and Crane, 1972), early silking (Hallauer and Sears, 1972; Troyer and Brown, 1972), prolificacy (Lonnquist, 1967; Kincer and Josephson, 1976; Mareck and Gardner, 1979; Coors and Mardones, 1989), seed size (Odhiambo and Compton, 1987), seedling emergence (Bell et al., 1983), reduction of pericarp thickness (Ito and Brewbaker, 1981), and resistance to earworm (Zuber et al., 1971).

Phenotypic recurrent selection also has been effective for improvement of a number of traits in sorghum. Investigations have shown improvements in seed size (Kwolek et al., 1986), resistance to cold injury (Livera and Carballo, 1976), tolerance to high soil temperatures at germination (Scheuring et al., 1978), acid soil tolerance (Duncan, 1981), and grain protein percentage (Ross et al., 1981).

Because selection is practiced on individuals, the plants (phenotypes) chosen are influenced only by environmental factors present during that specific growing season. Disadvantages of the selection process are manifested for traits that are largely influenced by different environmental conditions. Selection for superior genotypes can be ineffective due to phenotypic distortion caused by confounding environmental effects on trait(s) of interest.

Conflicting results from early studies using phenotypic recurrent selection were reported regarding relative success of the procedure. Sprague (1955) reasoned that lack of success observed in some studies could be due to: (1) parental control of only the male parent, (2) confounding effects on phenotypic expression due to genotype x environment interaction and soil variability, (3) subjective evaluation, (4) low heritability for traits of interest (especially grain yield), and (5) effects of inbreeding depression when the selected sample was small.

Subsequent quantitative genetic studies in maize indicated that considerable additive genetic variance was present for grain yield (Robinson et al., 1955). These studies sparked a renewed interest in phenotypic recurrent selection by researchers who had hopes of maximizing

the additive genetic variance through population improvement. However, distortion of genotypic expression by environmental influences remained a major problem affecting the selection for traits that exhibited low heritability. Experimental procedures were needed that would reduce the proportion of environmental variance and in turn increase heritability values.

Gardner (1961) reported on a procedure that he referred to as "modified mass selection". The procedure increased genotypic effects and reduced competition effects by optimizing environmental conditions and by spacing plants adequately within the row. Environmental effects also were reduced by superimposing small, uniform grids upon the field. Total environmental variance was partitioned into within-grid and between-grid components. An equal number of superior individuals would be selected from each grid. Selection within grids reduced the environmental variation due to differences in soil type, moisture, fertility, etc. Increased phenotypic variance combined with decreased environmental variance improved the precision of estimating heritability on a single plant basis. Gardner's technique helped alleviate some of the problems that were discussed previously by Sprague (1955).

Gardner (1961) reported yield improvement of 3.9% per cycle after the first four cycles of selection in 'Hays Golden' variety. After 15 cycles of selection, the grain yield of Hays Golden showed a linear increase of 3% per cycle (Gardner, 1977). The improvement slowed, however, after the 15th cycle (Mareck and Gardner, 1979). The authors reasoned that the lack of response observed in the later cycles was caused by

unfavorable genotype x environment interactions.

Since Gardner's introduction of the gridding process, many studies with maize have shown positive results using phenotypic recurrent selection techniques for grain yield. Johnson (1963) obtained 11% increase in grain yield per cycle after three cycles of selection in a tropical variety. Yield increased 7.42% in 'Kitale Composite Syn 3' after one cycle of selection (Eberhart et al. (1967). Darrah et al. (1978) reported gains of 1.13% per cycle for grain yield after ten additional cycles of selection in the same population. Yield improvements of 22.4% per cycle were reported by Barriga (1982) after two cycles of mass selection in a maize composite.

Hallauer and Wright (1967) reported increased yield of 1.5% per cycle after three cycles of phenotypic recurrent selection in 'Iowa Ideal'. Hallauer and Sears (1969) examined Iowa Ideal after two additional cycles of selection, and also the variety 'Krug' which had undergone six cycles of phenotypic recurrent selection. They obtained linear increases for grain yield of 1.4% and 1.6% per cycle, respectively. These values, however, were not statistically different from zero. Mulamba et al. (1983) examined Krug after eight additional cycles of phenotypic recurrent selection. A statistically significant linear increase for grain yield (0.49% per cycle) was reported from that study, although gain per cycle was smaller than the gains reported by Hallauer and Sears (1969). Mulamba et al. (1983) attributed the greater level of significance in their study to increased precision obtained by evaluating the progenies from different cycles in a larger number of environments.

Modifications of Gardner's grid system have been used successfully with different crops to maximize its potential under specific conditions applicable to the species of interest. Phenotypic recurrent selection for increased green weight of leaves was successful in tobacco (Nicotiana tobacum) (Matzinger and Wernsman, 1968). A linear response was obtained over four cycles of selection and an increase of 44 g/plant/cycle (4.29%) of green-leaf weight was realized. Burton (1974) used the term "recurrent restricted phenotypic selection" to describe the process he used for population improvement of Pensacola bahiagrass (Paspalum notatum). Four cycles of selection with that procedure increased forage yield in two populations by 2% and 6% per cycle. Fasoulas (1981) designed a form of gridded phenotypic recurrent selection that he referred to as the "honeycomb" method. Selection was practiced on widely spaced single plants arranged in a hexagonal pattern and grown under optimal field conditions. Fasoulas (1988) reported increased grain yields of 9% per cycle for rye (Secale cereale), 11% per cycle for corn, and 26% per cycle for sunflower (Helianthus annuus).

Phenotypic recurrent selection has been used in random-mating sorghum populations for improvement of grain yield. Doggett (1972a,b) reported results from eight random-mating populations advanced by using Gardner's gridded technique. The average gain in yield for the eight populations was 2.5% per cycle after three cycles of selection. Pollination control of female parents was obtained in some populations and control of both male and female parents was practiced in the others. Gains observed by using only female control ranged from zero to 32% and gains

from zero to 43% were found when both parents were controlled. Doggett (1988) pointed out that the original populations yielded significantly less than the check varieties 'Serena' and 'Dobbs', but advanced cycles of the populations improved by phenotypic recurrent selection yielded about the same as the checks.

Jan-orn (1973) tested one cycle of visual mass selection for individual-plant grain yield, using NP3R as the base population. Both male-fertile and male-sterile plants were selected within the grids. Evaluation of progenies showed that increased grain yield from the male-fertile panicles was 14% and the gain observed from male-sterile panicles was 6.8%. Patanothai et al. (1980, cited by Doggett, 1988) evaluated three types of recurrent selection methods using NP3R population. They found that grain yield increased 17.1% per season by using three cycles of female-choice mass selection for grain yield, 23.6% per season when alternating fertile and male-sterile plant mass selection was used, and 22.2% per season from one cycle of S_1 testing for yield.

Obilana and El-Rouby (1980a,b) reported large increases for grain yield in two sorghum random-mating populations improved by phenotypic recurrent selection. Grain yield increased 38.4% (12.8% per cycle) in one population and 40.4% (13.5% per cycle) in the other. Obilana (1985) tested both phenotypic recurrent selection and S_1 testing in two sorghum composites (composites B and Y). Both methods resulted in marked improvement for grain yield. In the B composite, yield increased 12.8% per cycle by using mass selection for yield over three cycles, and an increase in yield of 5.2% was shown for S_1 testing after one cycle of selection.

Three cycles of phenotypic recurrent selection increased grain yield 13.5% in the Y composite, and one cycle of S_1 testing produced a 40% increase in grain yield. When gain was based on a per-year basis, mass selection was more effective than S_1 testing in the B composite, and the two methods produced similar results in the Y composite.

Secrist (R. E. Secrist, Department of Agronomy, Iowa State University, Ames, Iowa, personal communication) compared the results from three cycles of phenotypic recurrent selection (for individual-panicle weight) and three cycles of replicated yield testing of S_1 families in two random-mating sorghum populations [IAP1R(M) and IAP4R(S1)] that were derived from the same base (C0) population. Grain yield increased 2.06% per cycle by using phenotypic recurrent selection and 2.99% when S_1 testing was used. The yield increases for both populations were statistically different from zero but they were not different from each other.

Direct selection for grain yield has been successful for improving random-mating sorghum populations over cycles of phenotypic recurrent selection. Improvement in grain yield often has been accompanied by changes in other traits not considered part of the selection criterion. An increase in plant height has been reported by several researchers (Doggett, 1972a,b; Jan-orn, 1973; Obilana and El-Rouby, 1980a,b; Patanothai et al., 1980, cited by Doggett, 1988). Doggett (1972b) reasoned that the increase in plant height was due to the superior competitiveness of tall plants in high planting densities. He suggested that future cycles should have wider plant spacings within rows to reduce the competition favoring tall plants. Delays in maturity when selection was

for grain yield were noted by Jan-orn (1973), but no significant differences in maturity were found by Doggett (1972a,b), Obilana and El-Rouby (1980a,b), and Patanothai et al. (1980, cited by Doggett, 1988) among cycles of populations selected by yield.

MATERIALS AND METHODS

Development of IAP2B(M) Population

IAP2B(M) is a broad-base random-mating sorghum population that provides a potential source of B-lines (fertility nonrestorer) in the A1 milo-kafir cytoplasmic-genetic male-sterility system. Development of the population was initiated in 1977 by making controlled crosses of ten inbreds (B-lines) onto bagged genetic male-sterile ($\underline{ms}_3$ $\underline{ms}_3$) panicles of the population NP2B (Atkins, 1982). Table 1 lists designations and pedigrees of the ten B-lines. NP2B provided a source of the $\underline{ms}_3$ genetic male-sterile gene in an agronomic type and genetic background preferable to that of the original 'Coes' source. Male parents of NP2B were 'Combine Kafir-60', 'Martin', 'Reliance', 'Westland', 'Wheatland', 'Redlan', 'Dwarf Redlan', and 'Tx606' (Nordquist et al., 1973). The component parental lines for both populations are adapted for production in midwest United States.

Equal weights of seed from the ten crosses were composited and approximately 6,000 plants of C0 were grown in isolation near Ames, Iowa, in 1978. The isolation planting consisted of 30 rows, each 30.5 m (100 ft) long, spaced 100 cm (40 in.) apart. Plants were spaced approximately 15 cm (6 in.) within the rows for optimum expression of each plant's genetic potential. Thirty equal-size rectangular cells [5 rows, 6.08 m (20 ft) long] were superimposed on the isolation plot.

IAP2B(M) was advanced each cycle by gridded mass selection for individual-panicle grain weight. Panicles that dispersed pollen at

Table 1. Inbred lines that were crossed onto bagged genetic male-sterile segregates of NP2B to initiate IAP2B sorghum population

Designation	Pedigree
Redbine 58	Martin x Combine 7008X-10
WD4	Dwarf Kafir x Rice Kafir-3-7-13
OKY54	Dwarf Redlan x Double #1-Short Kaura-2-1-E3-2
OKY55	Dwarf Redlan x Double #1-Short Kaura-19-3-1-1
KS12	Spur-Western Blackhull^3 x Redbine-60
KS18	White Martin x Short Kaura
KS22	Pink Kafir-Day x Westland
KS24	Spur-Western Blackhull^3 x Redbine-60
KS56	CK x (CK60^3 x H69-2 x Pioneer 846),F_6 (Greenbug resistant S. virgatum)
KS57	CK60 x (CK60^3 x H69-2 x Pioneer 846),F_6 (Greenbug resistant S. virgatum)

anthesis were identified by fastening a colored tag around the peduncle. All plants identified in C0 were fertile, with the genotype $\underline{MS}_3$ $\underline{ms}_3$. Selection was made for the largest 15 to 20 tagged panicles within each grid that ranged in height from about 100 to 150 cm (40-60 in.). No conscious selection was practiced for seed or panicle characteristics. Selected panicles were threshed individually and their grain weights recorded. Seed from ten panicles per cell with the highest grain weights (300 total panicles) was composited to establish the C1 population.

C1 and all subsequent cycle isolations were advanced by using the same procedures and criteria that were used for C0. Male-sterile segregates were present in these cycles of the population. In C1, only male-sterile plants were tagged at anthesis, but in advanced cycles (i.e., C2, C3, and C4), both male-fertile and male-sterile plants were identified. Different colored tags were secured around the peduncles at anthesis to distinguish the two fertility classes. Population advancement followed the same procedures and used the same selection strategies as described previously. The total number of male-sterile and male-fertile plants harvested in C1, C2, C3, and C4 were 606 and 0, 495 and 388, 451 and 453, and 456 and 457, respectively. In 1982, seed composites from male-fertile and male-sterile panicles were released to the public as IAP2B(M)C3.

Experimental Procedure

Experiments I and II were grown in Nicollet silty loam (fine-loamy, mixed, mesic Aquic Hapludoll) soil at the Iowa State University Agronomy and Agricultural Engineering Research Center near Ames, Iowa, in years 1984 through 1988. Isolation plantings of different cycles of IAP2B(M) were used as the seed source for replicated tests. The eight entries in Experiment I consisted of seed composites that were bulked from pollen-fertile panicles (S_1 families) of the C0, C2, C3, and C4, and from pollen-sterile panicles (half-sib families) of C1, C2, C3, and C4. In Experiment II, 120 S_1 families (derived from pollen-fertile panicles), 60 lines chosen randomly from the C0 and C4, were evaluated. Planting dates for both experiments in 1984, 1985, 1986, 1987, and 1988 were May 24, June 4,

May 21, May 22, and May 25, respectively.

Experimental units (plots) consisted of single 4.3 m (14 ft) rows spaced 102 cm (40 in.) apart. A center 3 m (10 ft) section comprised the experimental unit for grain yield and the components of yield. Plots were planted with a funnel planter at a high seeding rate to ensure good stands. At the 3 to 5 leaf growth stage, plots were thinned to one plant every 10.2 cm (4 in.), giving populations equivalent to 96,900 plants/ha (39,243 plants/acre).

Shortly after thinning, a center 2-m section of vigorous, uniformly spaced plants were marked in each plot by using colored garden stakes. If a suitable 3-m section could not be found, a shorter section was staked and the data obtained were converted to the equivalent of a 3-m plot. The number of plants within the area delineated by the garden stakes was recorded for each plot.

Number of days to midbloom stage and plant height were recorded only in 1986, 1987, and 1988. Plants were considered to be in midbloom stage when florets had opened half-way down the panicle. Plant height was recorded in centimeters as the mean of eight plants chosen randomly within each plot. Height of the main stalk was measured just before harvest, from soil surface to top of the panicle.

Plants were harvested each year between late September and mid-October, when grain moisture content of the entries ranged between 20 and 30%. Plants harvested were within the plot section marked by garden stakes. Panicles were severed just beneath the lowest panicle branch, placed in a cloth bag, and dried for three days at 60 C (140 F). As

each plot was harvested, the number of panicles was counted and then recorded on the harvest tag. Total weight of panicles for each plot was recorded to the nearest hundredth of a pound soon after drying.

Grain yields, expressed in Mg/ha, were estimated from total dry-panicle weights by using the method described by Robinson and Bernat (1963). A sample of six plots with total panicle weight above the mean of all entries and six plots with total panicle weight below the mean were threshed in an Almaco LPT All-Purpose Plot Thresher. A regression equation was then developed by using the threshed grain weights (Y) and total dry-panicle weights (X).

Let X_a = mean of six plots (i.e., different entries) with total dry-panicle weights above the mean of all plots,

X_b = mean of six plots with total dry-panicle weights below the mean of all plots,

Y_a = mean grain weight of six plots above the mean of all plots for total panicle weight x 1.465 (a factor to express grain yield on a Mg/ha basis),

Y_b = mean grain weight of six plots below the mean of all plots for total panicle weight x 1.465,

X = mean dry-panicle weight of the 12 selected plots,

Y = mean grain weight of the 12 selected plots,

$b = (Y_a - Y_b)/(X_a - X_b)$,

$a = Y - bX$,

$Y = a + bX$, the form of the completed regression equation.

The equations used to convert total panicle weight (lb/plot) to grain yield (Mg/ha) were:

Year	Experiment I	Experiment II
1984	Y = 0.131 + 0.79X	Y = -0.352 + 0.89X
1985	Y = 1.880 + 0.45X	Y = 0.190 + 0.75X
1986	Y = 0.687 + 0.20X	Y = -0.227 + 0.79X
1987	Y = -0.469 + 0.89X	Y = -0.603 + 0.92X
1988	Y = 0.0751 + 0.76X	Y = 1.930 + 0.42X

Seed size was determined as the weight in centigrams of 100 whole kernels sampled from the bulked seed of three panicles chosen at random within each plot. Number of panicles/plant was calculated by dividing number of panicles/plot by number of plants/plot. Number of seeds/panicle was derived by using the following equation:

$$\text{Seeds/panicle} = \frac{\text{Grain weight (g/plot)}}{\text{Panicles/plot x 100-seed wt (g)}} \times 100$$

Statistical Procedure - Experiment I

Field and laboratory data obtained for Experiments I and II were entered on a Hewlett-Packard Model 87 personal computer and uploaded to the Wylbur main-frame system of the Iowa State University Computation Center, Ames, Iowa. The data were analyzed by using SAS (Statistical Analysis System, SAS Institute Inc., Cary, North Carolina) procedures. Data presented for Experiment I include the means for entries grouped by cycles within families (S_1 and half-sib), mean squares from the analyses of variance, and estimates of total inbreeding depression.

Plots of the eight entries were replicated four times and arranged in a randomized complete-block design in each year. Seed composited from male-sterile panicles represent half-sib families, and seed composited from male-fertile panicles represent S_1 families (or lines). Years and replicates were considered random variables. Cycles and family types were considered fixed variables.

The linear model for the combined-year analysis of variance for Experiment 1 was:

$$Y_{ijkm} = u + Y_i + R(Y)_{ij} + F_m + C_{k(m)} + YF_{im} + YC_{ik(m)} + e_{ijk(m)}$$

where:

$i = 1 \ldots y$ years,

$j = 1 \ldots r$ replciations,

$k = 1 \ldots c$ cycles,

$m = 1 \ldots f$ family types,

Y_{ijkm} = observed value of the mth family within the kth cycle of the jth replication and ith year,

u = overall mean,

Y_i = effect of the ith year,

$R(Y)_{ij}$ = effect of the jth replicate within the ith year,

F_m = effect of the mth family type,

$C_{k(m)}$ = effect of the kth cycle within the mth family type,

YF_{im} = effect of the interaction of the ith year within the mth family type,

$YC_{ik(m)}$ = effect of the interaction of the ith year within the kth cycle within the mth family type,

$e_{ijk(m)}$ = experimental error.

The form for the analysis of variance, expected mean squares, and the appropriate F ratios for tests of significance are shown in Table 2 for the combined-year analysis of Experiment I.

Data from the S_1 and half-sib families were used to estimate inbreeding depression in Experiment I. The following formula:

$$\frac{XS1 - XHS}{XHS} \times 200 \quad ,$$

where XS1 = mean of S_1 families and XHS = mean of half-sib families, was used to estimate the total inbreeding depression that would be expected within the population. S_1 families descended from fertile panicles that were self-pollinated. Inbreeding depression, F = ½, was the result of one generation of self-pollination. Half-sib families were considered noninbred, F = 0, because they were derived from open-pollinated male-sterile panicles. Therefore, the difference between S_1 and half-sib family means for a given trait should estimate one-half of the total inbreeding depression.

Statistical Procedure - Experiment II

Parameters estimated from data obtained in Experiment II include mean squares from the analyses of variance, cycle means, frequency distributions of both cycles for each trait, variance components, heritability estimates, phenotypic and genotypic correlations, expected gain

Table 2. Form for the combined analysis of variance for Experiment I

Source of variation	df	Mean square	E(MS)	F test
Years (Y)	4	M1		M1/M2
Reps (R)/Y	15	M2		M2/M13
Entries (E)	7	M3	$\sigma^2 + r\sigma^2_{YE} + ry\Sigma E^2/(E-1)$	M3/M12
Families (F)	1	M4	$\sigma^2 + r\sigma^2_{YE} + rcy\Sigma F^2/(F-1)$	M4/M12
Cycles (C)/F	6	M5	$\sigma^2 + r\sigma^2_{YE} + ry\Sigma(C/F)^2/(CF-1)$	M5/M12
HS linear	1	M6	$\sigma^2 + r\sigma^2_{YE} + ry\Sigma(C_{HSL})^2/(C-1)$	M6/M12
HS quadratic	1	M7	$\sigma^2 + r\sigma^2_{YE} + ry\Sigma(C_{HSQ})^2/(C-1)$	M7/M12
HS cubic	1	M8	$\sigma^2 + r\sigma^2_{YE} + ry\Sigma(C_{HSC})^2/(C-1)$	M8/M12
S_1 linear	1	M9	$\sigma^2 + r\sigma^2_{YE} + ry\Sigma(C_{S1L})^2/(C-1)$	M9/M12
S_1 quadratic	1	M10	$\sigma^2 + r\sigma^2_{YE} + ry\Sigma(C_{S1Q})^2/(C-1)$	M10/M12
S_1 cubic	1	M11	$\sigma^2 + r\sigma^2_{YE} + ry\Sigma(C_{S1C})^2/(C-1)$	M11/M12
Y x E	28	M12	$\sigma^2 + r\sigma^2_{YE}$	M12/M13
Error	105	M13	σ^2	

from selection, and correlated response to character selection.

The 120 entries in Experiment II were arranged in a replicates-within-sets field design. There were six sets in each year, two replicates per set, with ten S_1 families from C0 and ten from C4 assigned randomly within each replicate. Effects attributable to sets were considered fixed, while effects due to the other sources of variation were considered random.

The linear model for each individual-year analysis in Experiment II was:

$$Y_{ijkm} + u + S_i + R_{j(i)} + C_k + L_{m(ik)} + e_{ijkm} ,$$

where:

$i = 1 \ldots s$ sets,

$j = 1 \ldots r$ replicates,

$k = 1 \ldots c$ cycles

$m = 1 \ldots g$ genotypes,

Y_{ijkm} = observed value for the mth genotype of the kth cycle cycle of selection within the ith set and the jth replicate,

u = overall mean,

S_i = effect of the ith set,

$R_{j(i)}$ = effect of the jth replicate within the ith set,

C_k = effect of the kth cycle of selection,

$L_{m(ik)}$ = effect of the mth genotype within the kth cycle of selection and the ith set,

i_{ijkm} = experimental error.

The linear model for the combined-year analysis of variance for Experiment II was:

$$Y_{hijkm} = u + Y_h + S_i + YS_{hi} + C_k + L_{m(ik)} + YL_{hm(ik)} + e_{hijkm} ,$$

where:

$h = 1 \ldots y$ years,

$i = 1 \ldots s$ sets,

$j = 1 \ldots r$ replicates,

k = 1 ... c cycles of selection,

m = 1 ... g genotypes,

Y_{ijkm} = observed value for the mth genotype in the kth cycle of selection within the ith set and the hth year,

u = overall mean,

Y_h = effect of the hth year,

S_i = effect of the ith set,

YS_{hi} = the effect of the interaction of the ith set with the hth year,

C_k = effect of the kth cycle of selection,

$L_{m(ik)}$ = effect of the mth genotype within the kth cycle of selection and the ith set,

$EL_{hm(ik)}$ = effect of the interaction of the hth year with the mth genotype nested within the ith set and kth cycle of selection,

e_{hijkm} = experimental error.

The form for the analysis of variance, expected mean squares, and the appropriate F ratios for tests of significance are shown in Table 3 for individual-year analyses and in Table 4 for the combined-year analyses.

Genotypic variance components for sources of variation attributable to C0/sets and C4/sets for each trait were estimated by using mean squares from the combined-year analysis of variance. The estimates of variance components were derived by using the following formulae:

$$\text{for C0} = \frac{\text{MS(C0/sets)} - \text{MS(C0/sets x years)}}{r\ y}$$

Table 3. Form for the individual-year analysis of variance for Experiment II

Source of variation	df	Mean square	Expected mean square	F test
Sets (S)	5	M1		
Replicates (R)/S	6	M2		
Genotypes (G)/S	114	M3	$\sigma^2 + r\sigma^2_{E/S}$	M3/M7
C0/S	54	M4	$\sigma^2_{C0} + r\sigma^2_{C0/S}$	M4/M8
C4/S	54	M5	$\sigma^2_{C4} + r\sigma^2_{C4/S}$	M5/M9
(C0 vs C4)/S	6	M6	$\sigma^2_{(C0C4)} + r\sigma^2_{(C0C4)/S}$	M6/M10
Experimental Error	114	M7	σ^2	
C0/S/R	54	M8	σ^2_{C0}	
C4/S/R	54	M9	σ^2_{C4}	
(C0 vs C4)/S/R	6	M10	$\sigma^2_{(C0C4)}$	

$$\text{for C4} = \frac{\text{MS(C4/sets)} - \text{MS(C4/sets x years)}}{r\ y}$$

where MS equals the appropriate mean square, r equals the number of replicates (2) and y equals the number of years (5).

Approximate confidence intervals ($1 - \alpha = 0.90$) for variance components were calculated by using procedures explained by Knapp et al. (1987). The following formulae were used to establish lower and upper confidence limits for the variance components:

Table 4. Form for the combined-year analysis of variance for Experiment II

Source of variation	df	Mean square	Expected mean square	F test
Years (Y)	4	M1		
Sets (S)	5	M2		
S x Y	20	M3		
Replicates (R)/S/Y	30	M4		
Genotypes (G)/S	114	M5	$\sigma^2 + r\sigma^2_{E/SY} + ry\sigma^2_{E/S}$	M5/M9
C0/S	54	M6	$\sigma^2_{C0} + r\sigma^2_{(C0)/SY} + ry\sigma^2_{C0/S}$	M6/M10
C4/S	54	M7	$\sigma^2_{C4} + r\sigma^2_{(C4)/SY} + ry\sigma^2_{C4/S}$	M7/M11
(C0 vs C4)/S	6	M8	$\sigma^2_{(C0C4)} + r\sigma^2_{(C0C4)/SY} + ry\sigma^2_{(C0C4)/S}$	M8/M12
G/S x Y	456	M9	$\sigma^2 + r\sigma^2_{E/SY}$	M9/M13
C0/S x Y	216	M10	$\sigma^2_{C0} + r\sigma^2_{(C0)/SY}$	M10/M14
C4/S x Y	216	M11	$\sigma^2_{C4} + r\sigma^2_{(C4)/SY}$	M11/M15
(C0 vs C4)/S x Y	24	M12	$\sigma^2_{(C0C4)} + r\sigma^2_{(C0C4)/SY}$	M12/M16
Experimental Error	570	M13	σ^2	
C0/S/Y x R	270	M14	σ^2_{C0}	
C4/S/Y x R	270	M15	σ^2_{C4}	
(C0 vs C4)/S/Y x R	30	M16	$\sigma^2_{(C0C4)}$	

lower interval: $[Mcy/(ry)][(F-F1)/F1 + (F2/F)(1-F2/F1)]$

upper interval: $[Mcy/(ry)][(F-F3)/F3 + (F4/F)(1-F4/F3)]$

where:

$F = Mc/Mcy$,

Mc = mean square for cycles/sets,

Mcy = mean square for cycles/sets x years,

r = number of replicates,

y = number of years,

$F1 = F(\alpha/2):df, ,$

$F2 = F(\alpha/2):df(f),df(fy),$

$F3 = F(1-\alpha/2):df,\infty,$

$F4 = F(1-\alpha/2):df(f),df(fy).$

Heritability values (H) were estimated on a progeny-mean basis for C0 and C4 as a ratio of genotypic variance to phenotypic variance. Formulae used for estimating H were:

$$H = \frac{[MS(cycles/sets)-MS(cycles/sets \times years)/ry]}{[MS(cycles/sets)/ry]}$$

$$= 1 - MS(cycles/sets \times years)/MS(cycles/sets)$$

where:

MS = the appropriate mean square,

r = number of replicates,

y = number of years.

Exact confidence intervals ($1 - \alpha = 0.90$) for the heritability estimates were calculated by using the procedures explained by Knapp et al. (1985, 1987). The following formulae were used to establish lower and

upper limits for the heritability estimates:

lower interval: $1 - F2/F$,

upper interval: $1 - F4/F$.

Definitions for F components were given previously for confidence intervals on variance components.

The equation used to calculate expected response to selection obtained by recombining selected families was:

Expected response per cycle: $\Delta G = k\ c\ \sigma ph\ H$

where:

ΔG = expected gain from selection,

k = standardized selection differential,

c = parental control value,

σph = square root of the phenotypic variance,

H = estimated heritability value.

Expected response for different selection procedures may be accommodated by modifying the values within the equation to coincide with the specific selection scheme being used. Expected response on a per-year basis can be calculated by dividing the estimated G value by the number of years necessary to complete one cycle of selection.

Phenotypic and genotypic correlations among traits were derived by using sums of squares from the combined analyses of variance and sums of cross products from the combined analyses of covariance obtained by using PROC MANOVA. The basic formulae were:

Phenotypic correlation:

$$r_p = \frac{MCPxy}{\sqrt{MSx}\ \sqrt{MSy}}$$

where:

MXPxy = mean cross product between trait x and y,

MSx = mean square for trait x,

MSy = mean square for trait y.

Genotypic correlation:

$$r_g = \frac{g(xy)}{\sqrt{\sigma^2 g(x)}\ \sqrt{\sigma^2 g(y)}}$$

where:

g(xy) = the genotypic covariance between traits x and Y,

$\sigma^2 g(x)$ = the genetic variance for trait x,

$\sigma^2 g(y)$ = the genetic variance for trait y.

Correlated response to selection was calculated by using the formula:

$$CRy(x) = kx\ \sqrt{Hx}\ rg(xy)\ \sigma g(y)$$

where:

CRy(x) = expected correlated response in trait y when selection is for trait x,

kx = standardized selection differential applied in selection for trait x,

$\sqrt{Hx}$ = square root of the heritability of trait x,

rg(xy) = genotypic correlation between traits x and y,

$\sigma g(y)$ = square root of the estimate of genotypic variance for trait y.

RESULTS

Environmental conditions generally were favorable for sorghum growth and development during 1984 through 1988. In the spring of 1984, ample moisture was available at planting time due to heavy snows the preceding winter and frequent spring rains. June and July were favorable for continued growth, but high temperatures and minimal rainfall were predominant in August. Adequate soil moisture at Ames permitted plants to reach maturity with good vigor, and mean grain yield for IAP2B was 5.94 Mg/ha (95 bu/A). Dry soil conditions prevailed during the spring of 1985 and planting was delayed two weeks beyond the usual date. Light rains and high soil temperatures initiated quick seedling emergence and good plant stands. Sparse rains fell throughout the summer, and the mean yield for IAP2B was only 4.45 Mg/ha (71 bu/A). Cool temperatures for about ten days followed planting in 1986, and plants were slow in emergence. High temperatures followed and abundant moisture created favorable conditions for sorghum growth and development. The mean yield for IAP2B was 6.20 Mg/ha (99 bu/A) in 1986. The 1987 planting also exhibited slow seedling emergence. However, high temperatures in June and July promoted rapid maturation, and plants reached pollination two weeks ahead of average. This trend continued through harvest where IAP2B displayed a mean grain yield of 5.00 Mg/ha (80 bu/A). Dry conditions existed at planting time in 1988, and soil moisture was barely sufficient for germination. Moisture was limited throughout the growing season, but timely rainfall combined with high temperatures promoted

vigorous growth. IAP2B had a mean grain yield of 6.07 Mg/ha (97 bu/A) in 1988.

Experiment I

The primary objective of Experiment I was to evaluate changes that occurred in IAP2B(M) during four cycles of gridded mass selection for individual-panicle grain weight. Eight entries, consisting of seed composites of half-sib families sampled from C1, C2, C3, and C4, and S_1 families from C0, C2, C3, and C4, were tested. Half-sib and S_1 progenies were obtained in each cycle isolation by harvesting male-sterile and male-fertile panicles, respectively. Means and values of inbreeding depression were estimated, and trends were examined.

The combined analyses of variance (Table 5) indicated that variation attributable to years was highly significant ($p < 0.01$) for grain yield, seeds/panicle, 100-seed weight, panicles/plant, and plant height, but it was not significant beyond $p < 0.05$ for days to midbloom. The mean squares for years, in most instances, were noticeably larger than those for other sources of variation for grain yield and the yield components. The variation due to replications/years was highly significant ($p < 0.01$) for grain yield, significant ($p < 0.05$) for plant height and days to midbloom, and nonsignificant (beyond $p < 0.05$) for seeds/panicle, 100-seed weight, and panicles/plant.

The entries source of variation showed highly significant ($p < 0.01$) differences for grain yield, panicles/plant, and plant height, but it did not display significance beyond $p < 0.05$ for seeds/panicle, 100-seed

Table 5. Mean squares and coefficients of variation from the combined analyses of variance for agronomic traits measured in Experiment I at Ames, Iowa during 1984-1988

Source of variation	df	Grain yield ($x10^{-1}$)	Seeds/ panicle ($x10^{-4}$)	100-seed weight ($x10^{-2}$)	Panicles/ plant ($x10^{-2}$)	df	Days to midbloom[a]	df	Plant height[b] ($x10^{-1}$)
Years (Y)	4	285.25**	337.17**	267.93**	184.73**	1	4.00	2	17.85**
Replications/Y	15	5.64**	6.66	3.23	3.66	6	3.61*	9	8.42*
Entries (E)	7	18.71**	4.43	12.77	11.88**	7	1.74	7	25.48**
Families (F)	1	119.22**	0.92	43.37*	49.62**	1	0.00	1	119.00**
Cycles/F	6	1.96	5.02	7.67	5.60	6	2.03	6	9.89*
HS linear	1	3.17	5.42	2.77	0.49	1	1.06	1	44.83**
HS quadratic	1	0.09	1.72	3.32	20.00*	1	0.78	1	0.01
HS cubic	1	0.01	1.01	4.43	0.81	1	0.01	1	0.24
S_1 linear	1	4.97	4.47	30.69*	2.24	1	3.31	1	3.84
S_1 quadratic	1	0.22	7.70	0.11	1.13	1	7.03*	1	10.21
S_1 cubic	1	3.29	9.79	4.71	8.91	1	0.01	1	0.20
E x Y	28	1.35	5.15	6.55	2.07	7	0.89	14	2.79
Error	105	1.80	4.27	7.16	3.01	42	1.47	63	3.54
CV (%)		7.49	12.43	10.38	11.14		1.84		5.01

[a]Measurements taken during 1987 and 1988.

[b]Measurements taken in 1986-1988.

*,**Indicate significance at the 5 and 1% levels of probability, respectively, in this table and all tables hereafter.

weight, and days to midbloom. Mean squares for the entry x year (i.e., genotype x environment) source of variation were not significant beyond $p < 0.05$ for any of the traits measured.

The sums of squares for entries were partitioned into variation due to family types (i.e., S_1 vs half-sib; designated families in Table 5) (1 df) and cycles within family types (6 df). Variation attributable to family types reflects differences due to inbreeding depression that were caused by one generation of selfing ($F=\frac{1}{2}$) in S_1 families as compared to open pollination ($F=0$) in half-sib families. Mean squares for families were highly significant ($p < 0.01$) for grain yield, panicles/plant, and plant height; significant ($p < 0.05$) for 100-seed weight; and nonsignificant (beyond $p < 0.05$) for seeds/panicle and days to midbloom. Variation due to cycles/families was significant ($p < 0.05$) for plant height, but it was not significant beyond $p < 0.05$ for the other characters measured.

The sums of squares for cycles/families were subdivided by using regression analysis. Linear, quadratic, and cubic effects indicate whether changes occurred in trait means over cycles and the nature of the changes when selection was based on individual-panicle grain weight. Half-sib families displayed highly significant ($p < 0.01$) linear effects for plant height and significant ($p < 0.05$) quadratic effects for panicles/plant. The half-sib families did not exhibit significance beyond $p < 0.05$ for the other traits measured. Significant ($p < 0.05$) linear effects for 100-seed weight and significant ($p < 0.05$) quadratic effects for days to midbloom were noted in S_1 families. Significant variations (beyond

$p < 0.05$) for S_1 families due to regression were not found for the other traits.

Entry means listed by family cycle (Table 6) portray the results discussed for the combined analysis of variance. Highly significant ($p < 0.01$) increases were evident upon perusal of the half-sib family means over cycles of selection for plant height (118.1, 120.5, 123.8, and 126.1 cm). The half-sib family means for panicles/plant (1.57, 1.68, 1.65, and 1.56) reinforce the significant ($p < 0.05$) quadratic regression indicated in Table 5. Significant ($p < 0.05$) linear progression for 100-seed weight and significant ($p < 0.05$) quadratic advancement for days to midbloom were supported by S_1 family means (2.46, 2.46, 2.58, and 2.60 g and 65.1, 66.4, 66.6, and 66.0, respectively). Other trends among the cycle means were noted, e.g., a linear improvement in grain yield for both half-sib and S_1 families. None of these trends, however, were statistically significant beyond $p < 0.05$.

Variation due to family type was highly significant for grain yield, panicles/plant, and plant height, and significant for 100-seed weight (Table 5). Table 7 lists character means by family type and estimates of total inbreeding depression. S_1 families exhibited lower means for grain yield, 100-seed weight, panicles/plant, and plant height compared to half-sib family means for the same traits. Magnitude of the inbreeding depression estimates for these traits (-18.2, -8.4, -13.7, and 11.5%, respectively) reflect the differences observed between the family type means.

Table 6. Means for entries grouped by family cycle for agronomic traits measured in Experiment I at Ames, Iowa during 1984-1988

Family cycle	Grain yield (Mg/ha)	Seeds/ panicle	100-seed weight (g)	Panicles/ plant	Days to midbloom[a]	Plant height[b] (cm)
HS-C1	5.85	1656	2.61	1.57	65.6	118.1
HS-C2	5.92	1630	2.63	1.68	66.1	120.5
HS-C3	5.99	1683	2.58	1.65	66.3	123.8
HS-C4	6.02	1716	2.68	1.56	66.1	126.1
S_1-C0	5.25	1641	2.46	1.52	65.1	112.3
S_1-C2	5.46	1745	2.46	1.54	66.4	116.4
S_1-C3	5.36	1630	2.58	1.44	66.6	116.7
S_1-C4	5.52	1609	2.60	1.51	66.0	114.9
LSD (0.05), cycles within HS or S_1 families	0.27	130	0.17	0.11	1.2	0.49

[a]Measurements taken during 1987 and 1988.

[b]Measurements taken during 1986-1988.

Table 7. Character means by family type, least significant difference, and estimates of total inbreeding depression from S0 to S∞ for agronomic traits measured in Experiment I at Ames, Iowa during 1984-1988

Character	Family type		LSD (0.05)	Inbreeding depression (%)	F test[a]
	$\bar{X}_{HS}$	$\bar{X}_{S1}$			
Grain yield (Mg/ha)	5.94	5.40	0.13	-18.2	**
Seeds/panicle	1671	1656	65	-1.8	ns
100-seed weight (g)	2.63	2.52	0.08	-8.4	*
Panicles/plant	1.61	1.50	0.05	-13.7	**
Days to midbloom[b]	66	66	0.6	0.0	ns
Plant height (cm)[c]	122	115	2.4	-11.5	**

[a] S_1 vs HS. ns = nonsignificant.

[b] Measured in 1987 and 1988.

[c] Measured during 1986-1988.

Experiment II

Data obtained for Experiment II were analyzed first on an individual-year basis, and then combined over the five years (1984-1988). Means for the individual-year data and their analyses of variance are presented in the Appendix for references (Tables A1 through A10).

The combined analyses of variance (Table 8) indicated that variation attributable to years was highly significant ($p < 0.01$) for grain yield, seeds/panicle, 100-seed weight, panicles/plant, days to midbloom, and plant height. The mean squares for years, in most instances, were appreciably larger than those for other sources of variation.

The genotypes/sets source of variation showed highly significant ($p < 0.01$) differences for all of the traits analyzed. The sums of squares for genotypes/sets were partitioned into variation due to C0/sets, C4/sets, and C0 vs C4/sets. Variations attributable to C0/sets and C4/sets were highly significant ($p < 0.01$) for all traits. Mean squares for the comparison of C0 vs C4/sets also exhibited highly significant ($p < 0.01$) differences for all characters.

The variation attributable to genotypes is displayed graphically by frequency distributions in Figures 1 through 6. Means for the 60 S_1 families in C0 and 60 S_1 families in C4 also are located on the figures for the traits measured. Table 9 presents parameters that aid in the description of the frequency distributions. The mean performance of S_1 families in C4 was significantly higher than the mean performance of S_1 families in C0 for grain yield, seeds/panicle, 100-seed weight, days to midbloom, and plant height, but it was significantly lower for panicles/

Table 8. Mean squares and coefficients of variation from the combined analyses of variance for agronomic traits measured in Experiment II at Ames, Iowa during 1984-1988

Source of variation	df	Grain yield ($x10^{-1}$)	Seeds/ panicle ($x10^{4}$)	100-seed weight ($x10^{-2}$)	Panicles/ plant ($x10^{-2}$)	df	Days to midbloom[a]	Plant height[a] ($x10^{1}$)
Years (Y)	4	1410.11**	1859.74**	1647.64**	947.23**	2	939.59**	88.49**
Sets (X)	5	25.36	35.01	25.52	69.08	5	3.85	67.22
Y x S	20	5.88	23.93	15.62	11.30	10	3.25	9.07
Reps (R)/S x Y	30	5.85	7.05	7.19	7.98	18	3.93	17.90
Genotypes (G)/S	114	13.17**	33.60**	58.67**	18.34**	114	24.13**	71.72**
C0/S	54	8.01**	30.36**	54.93**	19.50**	54	16.28**	52.03**
C4/S	54	15.75**	33.49**	54.44**	15.77**	54	25.90**	67.72**
C0 vs C4/S	6	36.37**	63.83**	130.51**	30.99**	6	78.74**	285.09**
G/S x Y	456	3.08**	6.46**	8.49**	3.60**	228	3.09**	5.24*
C0/S x Y	216	2.60**	5.38	8.21	2.90	108	2.61**	4.65
C4/S x Y	216	3.41**	7.05**	7.64**	4.17**	108	2.90**	6.14*
C0 vs C4/S x Y	24	4.42**	11.00*	18.80**	4.78	12	9.17**	2.53
Error	570	1.81	5.21	6.19	2.71	342	1.16	4.10
C0/S/Y x R	270	1.72	5.69	7.50	2.78	162	1.12	3.58
C4/S/Y x R	270	1.93	4.73	4.95	2.62	162	1.20	4.63
C0 vs C4/S/Y x R	30	1.59	5.16	5.53	2.95	18	1.29	4.07
CV (%)		7.70	13.78	9.97	10.84		1.59	5.46

[a]Measurements taken during 1985-1988.

Figure 1. Frequency distributions for the performance of 60 S_1 families from C0 and C4 for grain yield in Experiment II at Ames, Iowa during 1984-1988

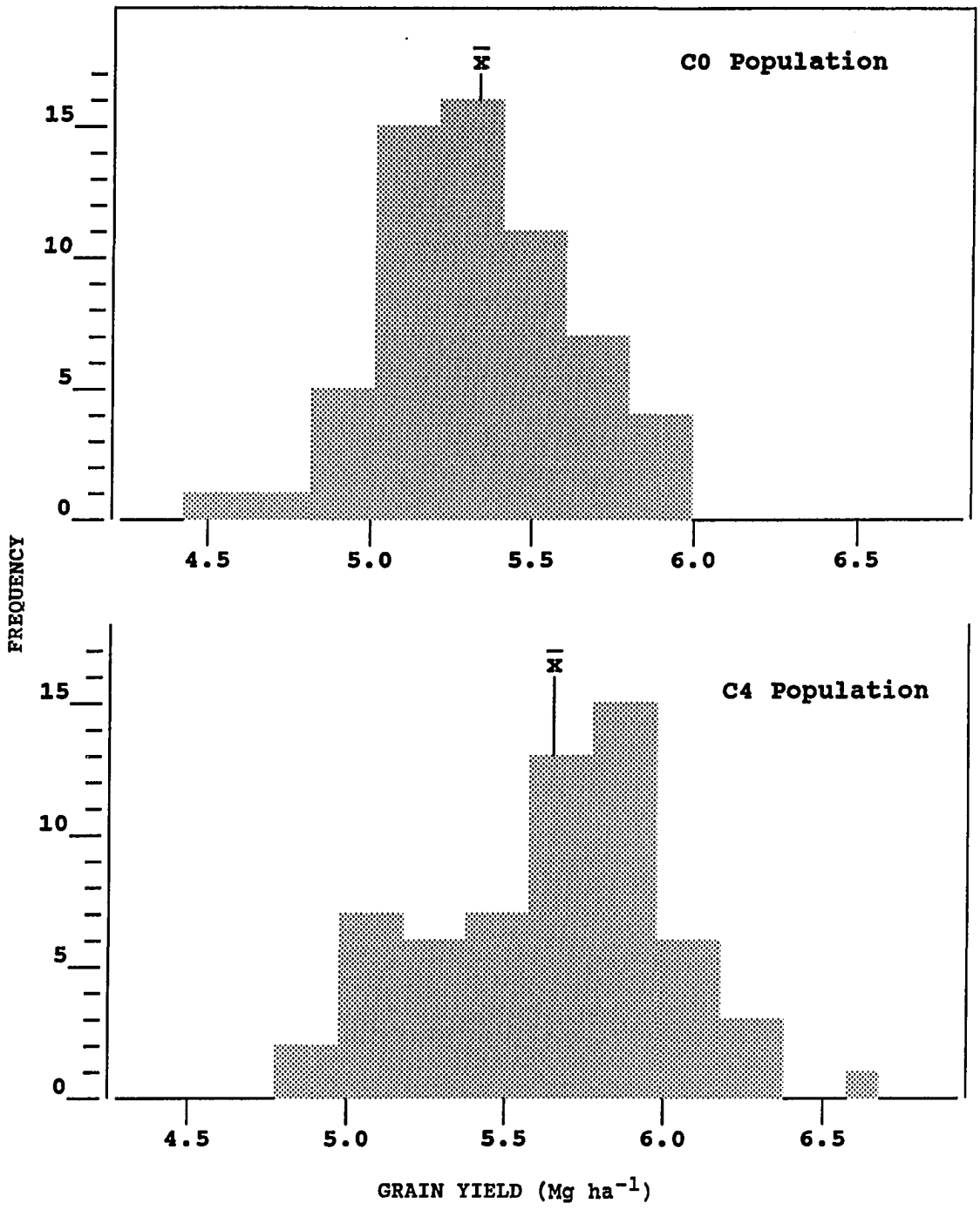
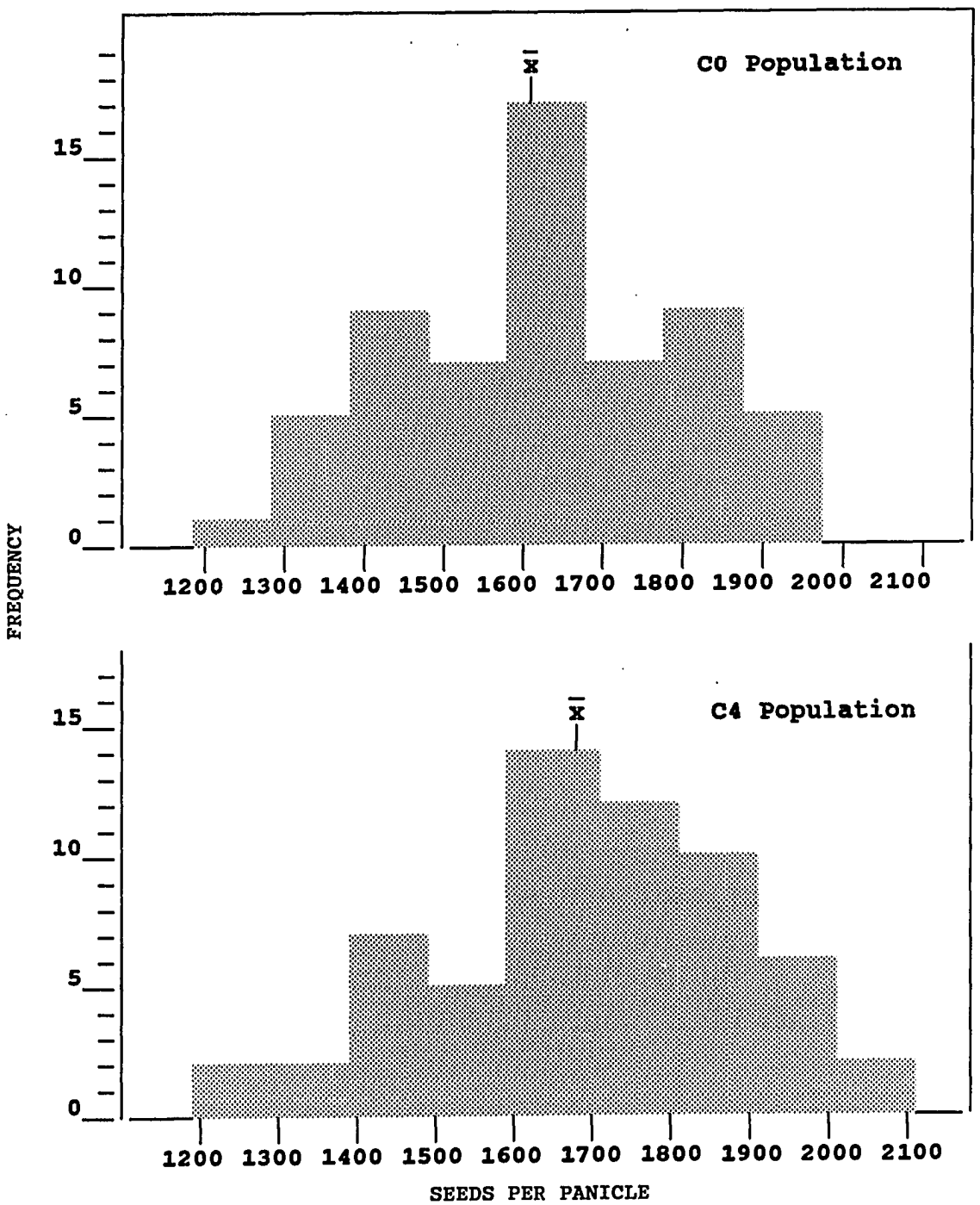

C0 Population
C4 Population
x̄
FREQUENCY
0
5
10
15
4.5
5.0
5.5
6.0
6.5
GRAIN YIELD (Mg ha-1)

Figure 2. Frequency distributions for the performance of 60 S_1 families from C0 and C4 for seeds/panicle in Experiment II at Ames, Iowa during 1984-1988


C0 Population
$\bar{x}$
15
10
5
0
1200 1300 1400 1500 1600 1700 1800 1900 2000 2100
C4 Population
$\bar{x}$
15
10
5
0
1200 1300 1400 1500 1600 1700 1800 1900 2000 2100
FREQUENCY
SEEDS PER PANICLE

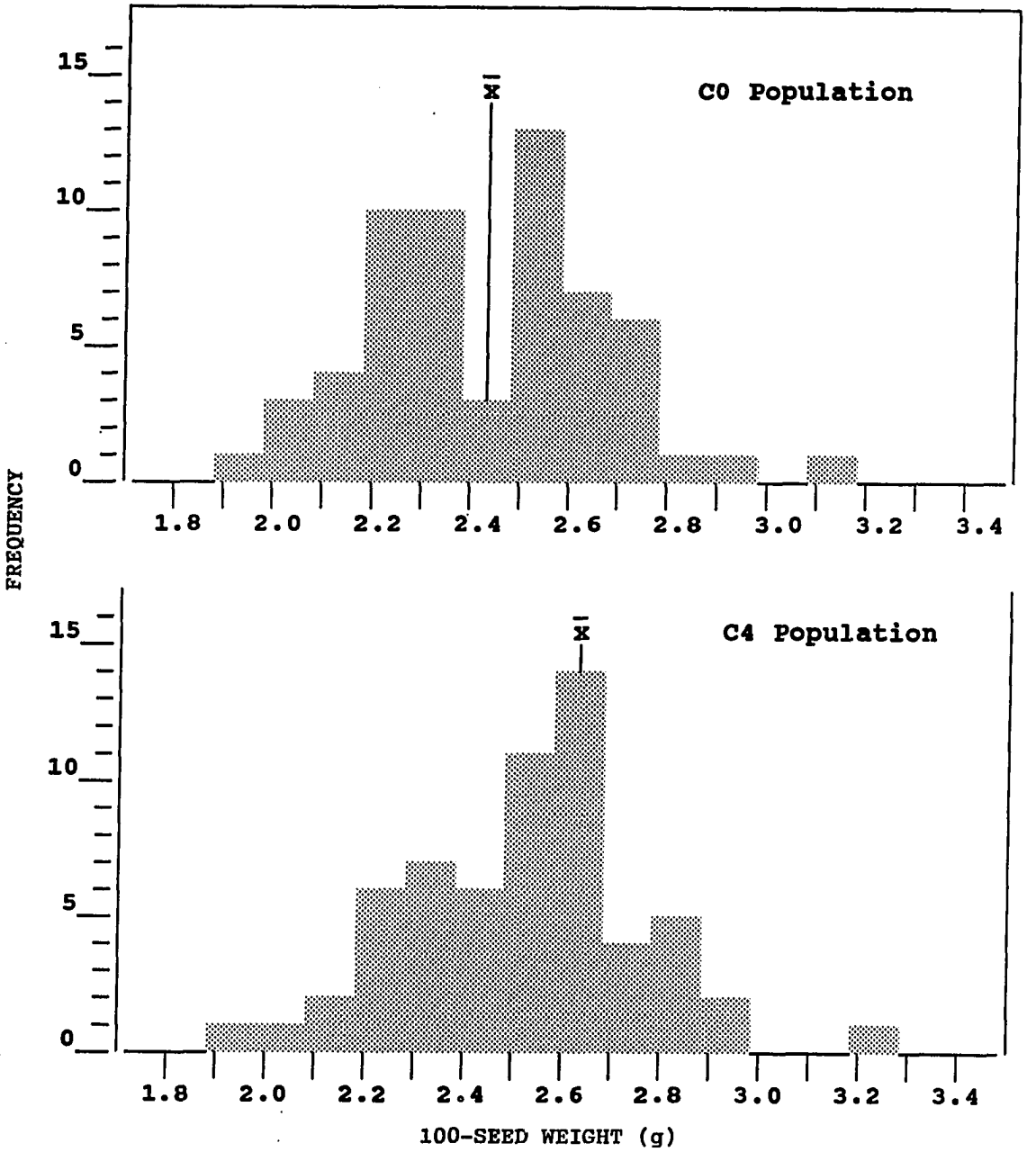
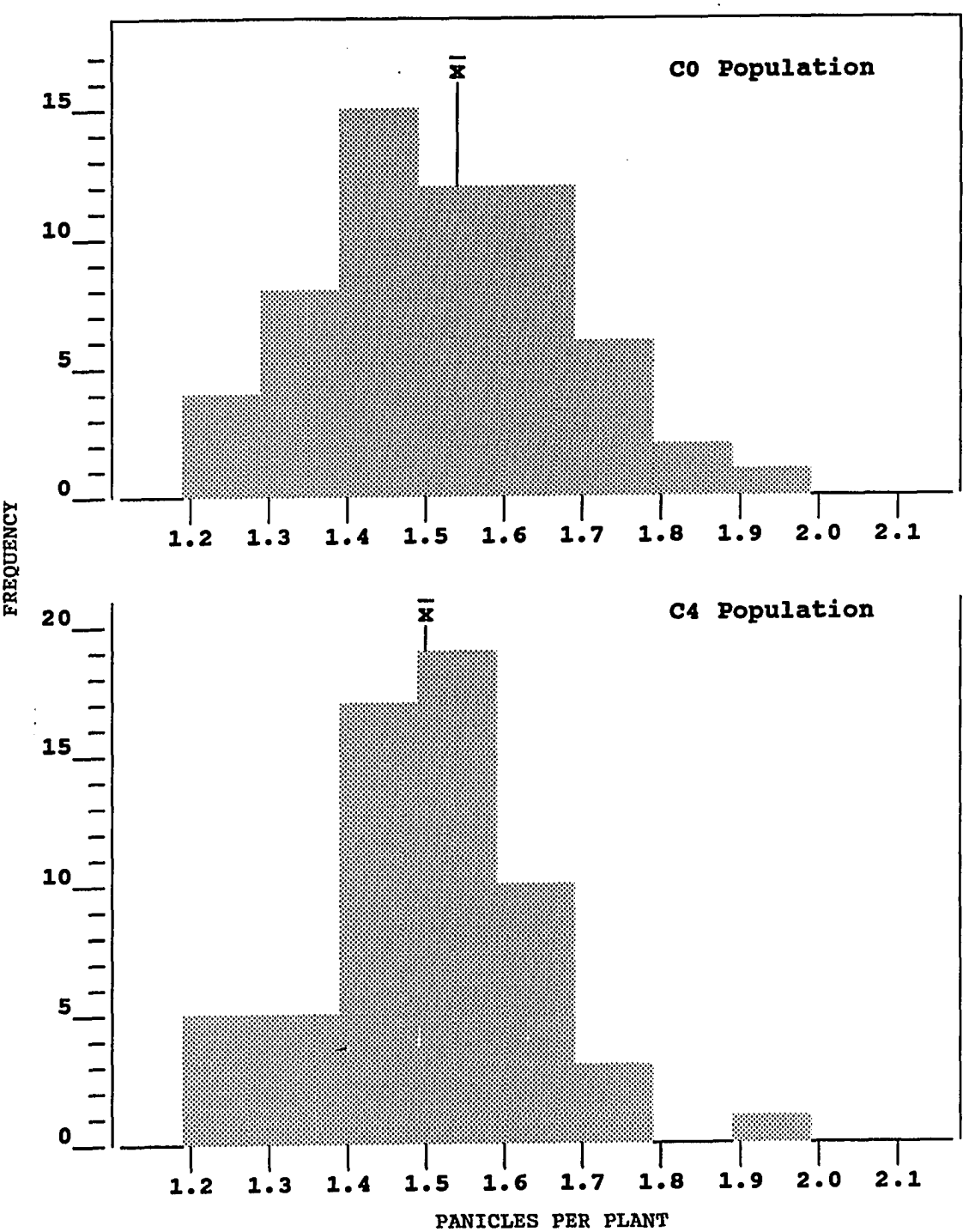


Figure 3. Frequency distributions for the performance of 60 S_1 families from C0 and C4 for 100-seed weight in Experiment II at Ames, Iowa during 1984-1988

Figure 4. Frequency distributions for the performance of 60 S_1 families from C0 and C4 for panicles/plant in Experiment II at Ames, Iowa during 1984-1988


C0 Population
C4 Population
FREQUENCY
PANICLES PER PLANT
0
5
10
15
20
1.2
1.3
1.4
1.5
1.6
1.7
1.8
1.9
2.0
2.1

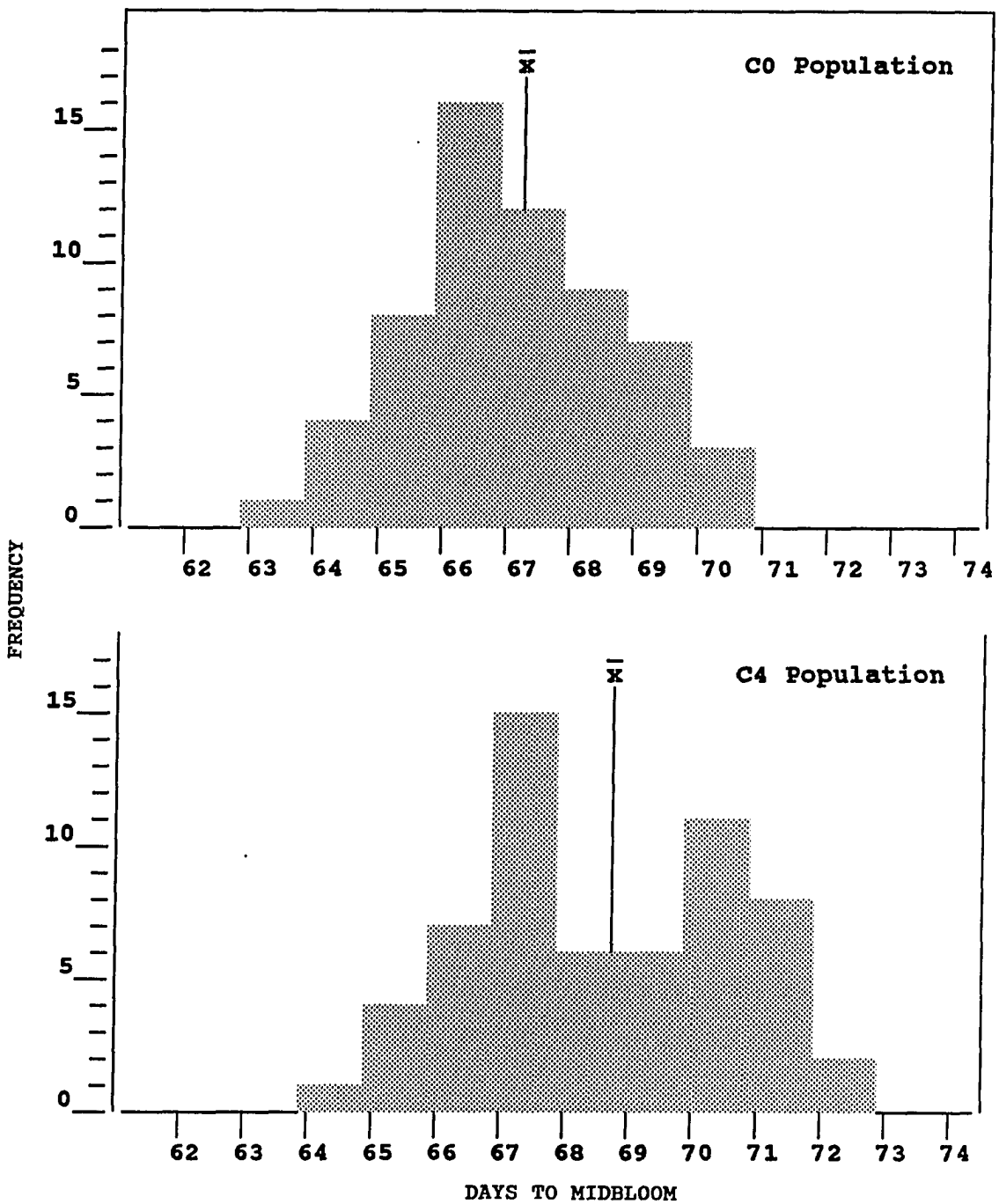


Figure 5. Frequency distributions for the performance of 60 S_1 families from C0 and C4 for days to midbloom in Experiment II at Ames, Iowa during 1986-1988

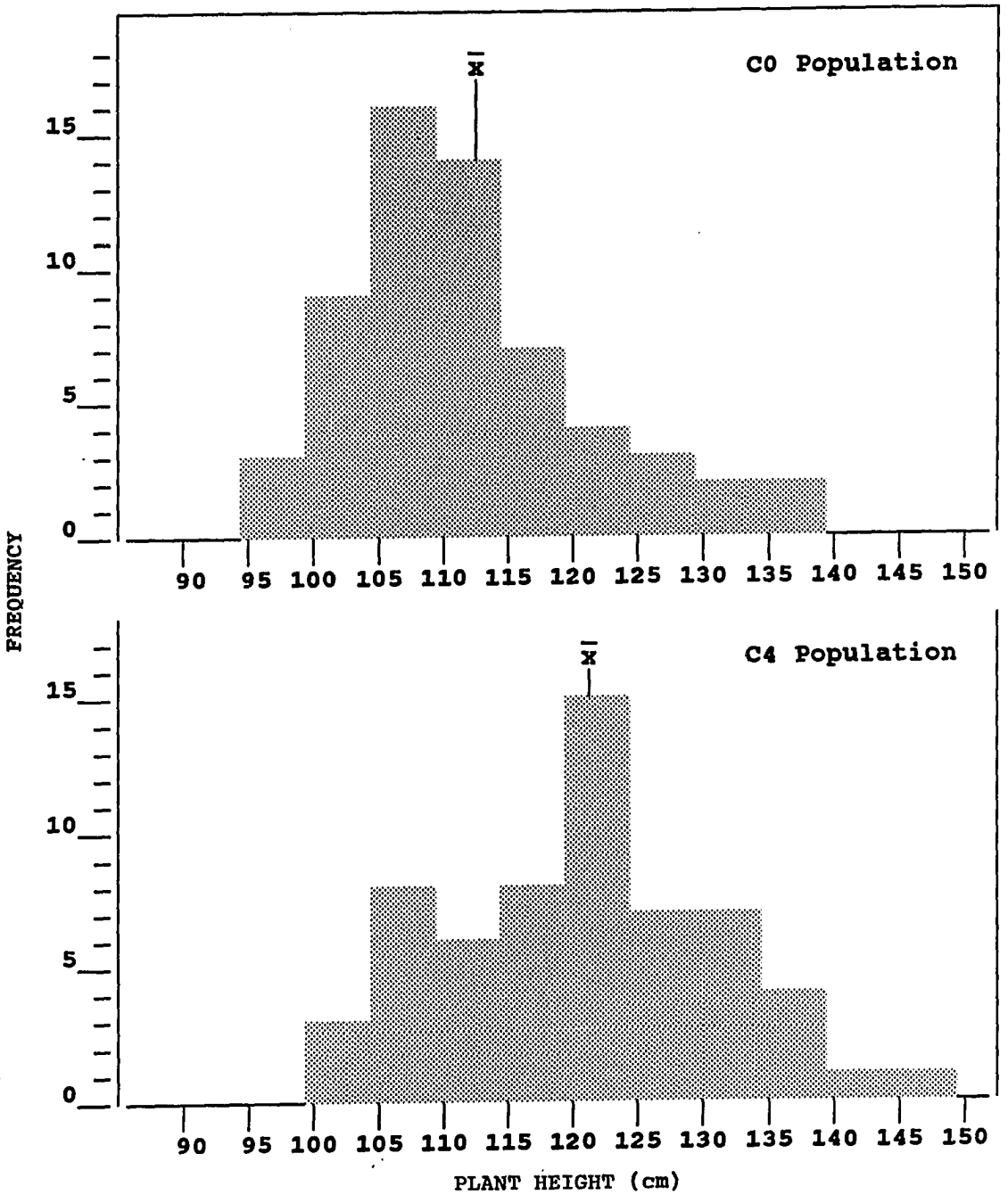


Figure 6. Frequency distributions for the performance of 60 S_1 families from C0 and C4 for plant height in Experiment II at Ames, Iowa during 1986-1988

Table 9. Means, standard errors, least significant differences, and high and low S_1 family values for agronomic traits measured in Experiment II at Ames, Iowa during 1984-1988

Trait and cycle of selection	Mean	LSD (0.05) C0 mean vs C4 mean	Low S_1 family value	High S_1 family value	LSD (0.05) among S_1 families
Grain yield (Mg/ha)					
C0	5.41 ± 0.017	0.048	4.51	6.08	0.374
C4	5.66 ± 0.018		4.89	6.66	
Seeds/panicle					
C0	1634 ± 10	26	1239	1967	200
C4	1679 ± 9		1244	2094	
100-seed weight (g)					
C0	2.45 ± 0.011	0.028	1.99	3.10	0.219
C4	2.54 ± 0.009		1.93	3.20	
Panicles/plant					
C0	1.53 ± 0.007	0.019	1.26	1.94	0.145
C4	1.51 ± 0.007		1.20	1.90	
Days to midbloom[a]					
C0	67.1 ± 0.32	0.73	63.2	70.2	5.62
C4	68.7 ± 0.36		64.5	72.5	
Plant height (cm)[a]					
C0	113 ± 0.056	0.122	97	139	0.948
C4	122 ± 0.058		103	148	

[a]Measurements taken during 1986-1988.

plant. The range in performance from the low S_1 family value to the high S_1 family value increased from C0 to C4 for grain yield (from 1.57 to 1.77 Mg/ha), seeds/panicle (from 728 to 850), 100-seed weight (from 1.11 to 1.27 g), panicles/plant (from 0.68 to 0.70), days to midbloom (i.e., from 7.0 to 8.0), and plant height (from 42 to 45 cm).

Table 8 shows that the genotypes/sets x years (i.e., genotype x environment) interaction was highly significant ($p < 0.01$) for grain yield, the components of yield, and days to midbloom, and that it exceeded the $p < 0.05$ level of probability for plant height. The genotypes/sets x years sums of squares were partitioned into sources of variation attributable to C0/sets x years, C4/sets x years, and C0 vs C4/sets x years. The C0/sets x years interaction was highly significant ($p < 0.01$) for grain yield and days to midbloom, but it was not different beyond $p < 0.05$ for seeds/panicle, 100-seed weight, panicles/plant, and plant height. Variation attributable to the C4/sets x years interaction was highly significant ($p < 0.01$) for grain yield, seeds/panicle, 100-seed weight, panicles/plant, and days to midbloom, and it exceeded the $p < 0.05$ level of probability for plant height. The C0 vs C4/sets x years interaction was highly significant ($p < 0.01$) for grain yield, 100-seed weight, and days to midbloom, but it was not significant beyond the $p < 0.05$ probability level for panicles/plant or plant height.

The proportions of total phenotypic variation attributable to genotypic, genotype x environment, and experimental error variance components are given in Figure 7 for agronomic traits measured in C0 and C4. Estimates of genotypic variance with approximate confidence intervals

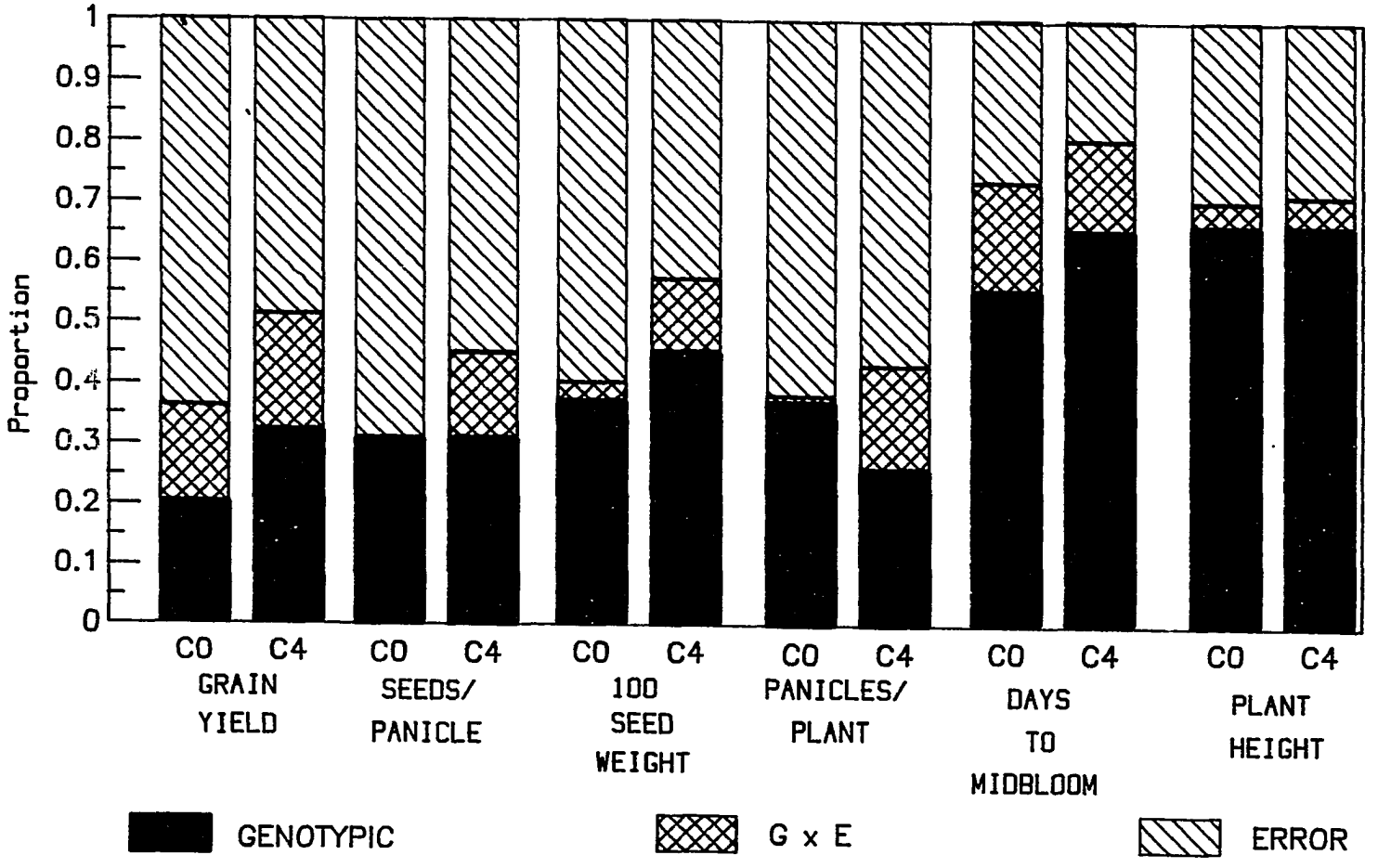


Figure 7. Proportion of the total variance contributed by genotypic, genotype x environment interaction, and experimental error components for 60 S_1 families from C0 and C4 of IAP2B(M) population in Experiment II

($1 - \alpha = 0.90$) are presented in Table 10. Genotypic variance among S_1 families increased significantly (as established by confidence intervals at $1 - \alpha = 0.90$) from C0 to C4 for grain yield and days to midbloom. Differences observed for variance component estimates between C0 and C4 for the other characters did not surpass limits established by the confidence intervals at the $1 - \alpha = 0.90$ level.

Heritability estimates on a progeny-mean basis with exact confidence intervals are shown numerically in Table 10 and graphically in Figure 8. The estimates of heritability were high for most traits. Grain yield for C0 had the lowest value ($H = 0.68$) and plant height for C0 was the highest ($H = 0.91$). Heritability estimates increased for grain yield from C0 to C4 (from 0.68 to 0.78), but they decreased for panicles/plant (from 0.85 to 0.74). These differences were statistically significant in accordance with exact confidence intervals at $1 - \alpha = 0.90$. Estimates of heritability for the other characters differed between C0 and C4, but the differences did not surpass limits established by using confidence intervals at a probability level of $1 - \alpha = 0.90$.

Expected response from S_1 family selection using replicated yield trials and the actual gains that were realized by using gridded mass selection for threshed panicle weight are presented in Table 11. Expected gains were derived by using variance component and heritability estimates from Table 10 along with a 10% selection intensity value (i.e., 1.75). Expected gain/year for grain yield by using S_1 family selection increased markedly based on C0 vs C4 data (from 2.0% to 3.2% of the mean), but it decreased appreciably for panicles/plant (from 4.5% to 3.6% of

Table 10. Genotypic variance component estimates with approximate confidence intervals (1 - α = 0.90) and heritability (H) estimates on a progeny-mean basis with exact confidence intervals (1 - α = 0.90) for agronomic traits in Experiment II at Ames, Iowa during 1984-1988

Trait and cycle of selection	Genotypic variance	Confidence intervals			Heritability (H)	Confidence intervals		
		Lower limit	Upper limit	Width		Lower limit	Upper limit	Width
Grain yield (Mg/ha)								
C0	0.054[a]	0.033	0.088	0.055	0.6754[a]	0.5465	0.7777	0.2312
C4	0.123	0.083	0.189	0.106	0.7832	0.6971	0.8515	0.1544
Seeds/panicle								
C0	24981	17262	37678	20416	0.8229	0.7526	0.8787	0.1261
C4	26554	17900	40458	22558	0.7896	0.7060	0.8559	0.1499
100-seed weight (g)								
C0	0.047	0.033	0.070	0.037	0.8506	0.7913	0.8977	0.1064
C4	0.047	0.033	0.070	0.037	0.8597	0.8040	0.9039	0.0999
Panicles/plant								
C0	0.017	0.012	0.025	0.013	0.8513[a]	0.7923	0.8982	0.1059
C4	0.012	0.008	0.018	0.010	0.7353	0.6302	0.8187	0.1885
Days to midbloom[b]								
C0	2.28[a]	1.59	3.41	1.83	0.8398	0.7668	0.8932	0.1264
C4	3.83	2.74	5.64	2.90	0.8880	0.8369	0.9253	0.0884
Plant height (cm)[b]								
C0	79.0	57.0	115.2	58.2	0.9106	0.8699	0.9404	0.0705
C4	102.6	74.0	149.8	75.8	0.9093	0.8680	0.9395	0.0715

[a]Estimates of genotypic variance and H among C0 and C4 were significantly different in accordance with confidence intervals (1 - α = 0.90).

[b]Measurements taken during 1986-1988.

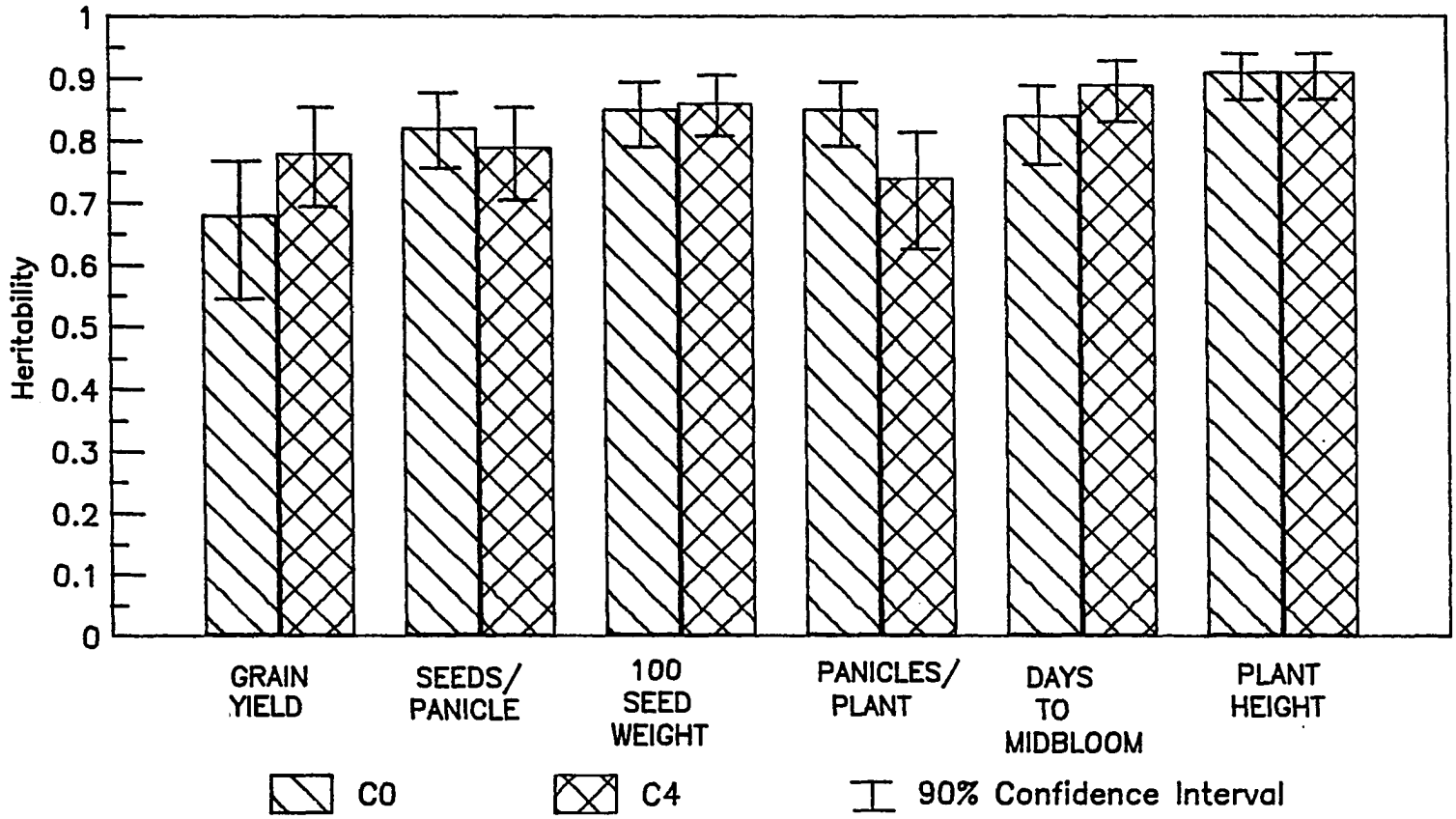


Figure 8. Heritability estimates on a progeny-mean basis with exact confidence intervals ($1 - \alpha = 0.90$) for agronomic traits in Experiment II at Ames, Iowa during 1984-1988

Table 11. Expected gain from S_1 family selection for grain yield in replicated trials and realized gain after four cycles of gridded mass selection for individual-panicle grain weight for agronomic traits in Experiment II at Ames, Iowa during 1984-1988

Trait and cycle of selection	Expected from S_1 family selection (with 3 yrs/cycle)			Realized from gridded mass selection (with 1 yr/cycle)	
	Gain/ cycle	Gain/ year	Gain/year (% of mean)	Gain/ cycle	Gain/year (% of mean)
Grain yield (Mg/ha)					
C0	0.33	0.11	2.0		
C4	0.54	0.18	3.2	0.06	1.2
Seeds/panicle					
C0	251	83.6	5.1		
C4	253	84.3	5.0	11.3	0.7
100-seed weight (g)					
C0	0.349	0.116	4.7		
C4	0.351	0.117	4.6	0.023	0.9
Panicles/plant					
C0	0.21	0.069	4.5		
C4	0.16	0.054	3.6	-0.005	-0.3
Days to midbloom[a]					
C0	2.4	0.81	1.2		
C4	3.2	1.08	1.6	0.4	0.6
Plant height (cm)[a]					
C0	14.8	4.9	4.3		
C4	16.9	5.6	4.6	2.25	2.0

[a]Measurements taken during 1986-1988.

the mean). Differences between C0 and C4 for expected gains were considerably smaller for the other traits. Empirical values are listed for gains determined after four cycles of gridded mass selection for individual-panicle grain yield. These values offer a comparison between gains predicted for S_1 testing and actual gains realized from mass selection in IAP2B. Gains observed from mass selection were considerably smaller for all traits than the gains estimated for S_1 family selection.

Phenotypic and genotypic correlations among agronomic characters are given in Table 12. Among the S_1 families of C0, the phenotypic correlations ($r = 0.44$) between grain yield and days to midbloom was significant ($p < 0.01$). Seeds/panicle showed negative correlation ($p < 0.01$) with 100-seed weight ($r = -0.56$), panicles/plant ($r = -0.56$), and plant height ($r = -0.54$). Plant height was correlated positively ($p < 0.01$) with 100-seed weight ($r = 0.43$) and panicles/plant ($r = 0.38$).

Among the S_1 families of C4, grain yield exhibited positive correlations ($p < 0.01$) with seeds/panicle ($r = 0.49$), panicles/plant ($r = 0.38$), and days to midbloom ($r = 0.41$). Seeds/panicle was negatively correlated ($p < 0.01$) with 100-seed weight ($r = -0.65$) and plant height ($r = -0.46$). 100-seed weight was negatively correlated ($p < 0.05$) with panicles/plant ($r = -0.30$), but it was correlated positively ($p < 0.05$) with plant height ($r = 0.34$). Panicles/plant and plant height showed a positive correlation ($r = 0.38$). Genotypic correlations most often were larger than the corresponding phenotypic correlation, although relative magnitudes of the coefficients usually were similar.

Table 12. Phenotypic (above diagonal) and genotypic (below diagonal) coefficients of correlation among agronomic traits in C0 and C4 of Experiment II at Ames, Iowa during 1984-1988

Trait and cycle of selection	Grain yield	Seeds/ panicle	100-seed weight	Panicles/ plant	Days to midbloom	Plant height
Grain yield						
C0		0.12	0.25	0.17	0.44**	0.05
C4		0.49**	-0.13	0.38**	0.41**	0.07
Seeds/panicle						
C0	0.08		-0.56**	-0.56**	0.26	-0.54**
C4	0.53		-0.65**	-0.18	0.17	-0.46**
100-seed weight						
C0	0.28	-0.54		-0.17	-0.12	0.43**
C4	-0.15	-0.64		-0.30*	-0.11	0.34*
Panicles/plant						
C0	0.15	-0.61	-0.21		-0.03	0.38**
C4	0.43	-0.15	-0.37		0.15	0.38**
Days to midbloom[a]						
C0	0.55	0.26	-0.15	-0.05		-0.04
C4	0.50	0.20	-0.15	0.23		0.20
Plant height[a]						
C0	0.12	-0.63	0.52	0.48	-0.04	
C4	0.13	-0.53	0.37	0.51	0.20	

[a]Measurements taken during 1986-1988.

Selection for a specific trait may create changes for statistical parameters related not only to the trait under selection, but it can also cause alterations for traits that are not considered a direct criterion of selection. Expected response in unselected traits was estimated when selection was for grain yield, the components of grain yield, plant height, and days to midbloom (Table 13). Responses are expressed as a percentage of the expected response to direct selection for a given trait. Based on data from the base population (C0), selection for grain yield would be expected to reflect a moderate increase in days to midbloom and small increases in seeds/panicle, 100-seed weight, panicles/plant, and plant height. Correlated responses of unselected characters based on data from C4, when selection was for grain yield, were somewhat different than those noted for C0. The responses for seeds/panicle and panicles/plant were much greater for C4, but the response for 100-seed weight was estimated to be lower for C4.

Indirect selection for grain yield by selecting for a yield component, days to midbloom, or plant height lacks strong support from the expected responses listed in Table 13. Moderate gains would be expected for grain yield based on both the C0 and C4 results if selection was for days to midbloom. Expected response for grain yield changed both in magnitude and direction from the C0 to C4 data when selection was for other traits. Selection for seeds/panicle, based on the C0 data, would be expected to reflect a small decrease in grain yield, but the C4 data indicated there would be a moderate increase in yield. Selection for 100-seed weight would be expected to provide a small increase in grain

Table 13. Expected correlated response in other traits when S_1 family selection is for grain yield, seeds/panicle, 100-seed weight, panicles/plant, days to midbloom, and plant height determined from Experiment II at Ames, Iowa during 1984-1988[a]

Trait and cycle of selection	Unselected trait					
	Grain yield	Seeds/ panicle	100-seed weight	Panicles/ plant	Days to midbloom	Plant height
Grain yield						
C0	100.0	6.2	20.5	10.8	40.1	8.5
C4	100.0	48.3	-13.2	40.9	42.8	10.8
Seed/panicle						
C0	-9.0	100.0	-51.0	-57.7	24.8	-57.2
C4	49.4	100.0	-56.8	-12.4	17.4	-45.8
100-seed weight						
C0	29.7	-51.0	100.0	-19.2	-13.9	47.0
C4	-15.2	-64.1	100.0	-37.0	-14.2	34.8
Panicles/plant						
C0	16.0	-59.8	-19.9	100.0	-4.5	44.4
C4	37.9	-13.4	-31.0	100.0	18.7	41.8
Days to midbloom[b]						
C0	53.1	27.7	-13.6	-5.2	100.0	-4.4
C4	55.4	20.2	-15.4	27.8	100.0	20.4
Plant height[b]						
C0	12.3	-69.4	49.8	55.6	-4.1	100.0
C4	14.3	-54.5	38.7	63.8	19.9	100.0

[a]Responses are expressed as percentages of the expected gain from S_1 family selection for a given character.

[b]Measurements taken during 1986-1988.

yield based on the C0 data, but it would be expected to decrease grain yield slightly according to the C4 results. The estimates of correlated response presented in Table 13 indicated that selection for any one trait likely would have only moderate effect on the response for any of the other characters.

DISCUSSION

IAP2B(M)C4 was formed from elite inbred maintainer (for A1 cytoplasm) lines that were advanced four cycles by using mass selection for individual-panicle grain weight. The population was initiated to augment the elite B-line germplasm base adapted for grain sorghum production in northern segments of midwest United States. Harvey (1977) revealed that hybrids of one seed parent, 'Wheatland', accounted for 45% of the reported grain sorghum acreage under production at that time. Female parents used throughout much of the sorghum production area often produced hybrids that matured too late for effective use in Iowa. Relatively short-term projects were needed to diversify and restructure combinations of genes that could be used as seed parents for hybrid sorghum production in that region. An improved random-mating population formed from elite parents should increase the proportion of favorable individuals that contain the wide array of different genes and gene combinations needed to diversify the sorghum germplasm available. Two experiments were conducted to evaluate the breeding potential of IAP2B population *per se* and also to examine changes that occurred throughout the selection process.

A favorable shift in mean performance for the trait under selection is one goal of recurrent selection. In Experiment I, grain yield of composites of S_1 families increased from 5.25 Mg/ha in C0 to 5.52 Mg/ha in C4. The difference (.27 Mg/ha) was equivalent to the LSD value calculated (at $p < 0.05$) for differences between cycle means within half-sib or S_1 families (Table 6). Grain yields of the individual S_1 families

in Experiment II showed a similar response to selection. The yield increase of 0.25 Mg/ha from C0 to C4 (Table 9) was highly significant ($p < 0.01$) in accordance with the F ratio (Table 8) calculated for C0/sets vs C4/sets. Compared to the base population in each experiment, grain yield increased 1.28% per cycle in Experiment I and 1.15% per cycle in Experiment II over four cycles of selection. Regression analyses in Experiment I (Table 5) did not distinguish a specific type of response in association with the increased grain yield observed among composites of S_1 or half-sib families.

Half-sib family composites evaluated in Experiment I showed moderate but steady gains for mean grain yield from C1 through C4 (Table 6). However, neither the partitioning of types of regression nor the differences among cycle means within half-sib families displayed significance beyond $p < 0.05$. Additional replication of the half-sib and S_1 family composites in each cycle would have allowed for higher precision of the estimates of mean grain yield over cycles, and increased the degrees of freedom for the F-test.

Recurrent selection for one trait often creates changes in other traits that were not included in the selection strategy. In Experiment II, highly significant ($p < 0.01$) differences for mean performance of S_1 families between C0 and C4 were displayed for all traits measured. The four cycles of selection for threshed-panicle weight increased seeds/panicle, 100-seed weight, days to midbloom, and plant height, but decreased panicles/plant. Regression analyses for these traits (Experiment I), however, did not display a consistent association with any of

the types of regression over cycles and family structure (Table 5). Few traits exhibited a significant ($p < 0.05$) response for any of the types of regression. A larger sample of germplasm within each cycle-family population may have served more effectively to measure the response to selection over cycles. Experiment II provided greater precision for differentiation of the performance of C0 and C4 because of the larger sample of plants for each S_1 family. The difference required for statistical significance ($p < 0.01$) in Experiment II for panicles/plant was only two-hundredths of one panicle per plant. Although statistically significant, the decrease of panicles/plant in C4 almost certainly would have little effect on performance relative to the C0 population. Differences between C0 and C4 also were highly significant ($p < 0.01$) for seeds/panicle (45), 100-seed weight (0.09 g), days to midbloom (1.6), and plant height (9 cm). The magnitudes of these differences are moderate as well, and likely are of minor consequence. Progression of these trends over additional cycles, however, may lead to differences that could have practical consequence agronomically.

Phenotypic expression of a trait is the result of genetic and environmental influences combined with genotype by environment interactions. These sources of variation can be partitioned by analyzing replicated experiments that were grown in multiple environments. In Experiment II, differences attributable to years (environments) were highly significant ($p < 0.01$) for all traits (Table 8). Environmental influences, therefore, exerted a measurable and large effect on the phenotypic expression of agronomic traits among the S_1 families of IAP2B in

that experiment. In Experiment I, the genotype by environment interaction was not significant (beyond $p < 0.05$) for any of the characters evaluated (Table 5).

The interaction of C0 vs C4/sets by years in Experiment II was highly significant ($p < 0.01$) for grain yield. Appendix Tables A1 through A5 list C0 and C4 means for agronomic traits evaluated each year in Experiment II. Mean grain yield of the S_1 families in C4 was higher than the mean for C0 in all five years. The variation attributable to genotype by environment interaction, therefore, was a reflection of differences in magnitude between the C0 and C4 means, rather than differences in ranking.

The comparison, C0 vs C4/sets by years, also was highly significant ($p < 0.01$) for seeds/panicle, 100-seed weight, and days to midbloom, but it was not significant (beyond $p < 0.05$) for panicles/plant and plant height (Table 8). Thus, genotype by environment interactions were not critical in the phenotypic expression for panicles/plant and plant height, but significant changes in magnitude of the C0 vs C4 comparison were observed over the years summarized for the other traits (Table A1 through Table A5). Cycle means for seeds/panicle and 100-seed weight (Tables A1 through A5) displayed differences in both magnitude and rank over the five years. Mean grain yields of genotypes from C4 were consistently higher than the mean yields of genotypes from C0, but interactions among individual genotypes and environments determined the impact of seeds/panicle and 100-seed weight on their yielding ability.

The first goal of recurrent selection, a favorable shift in the

mean for grain yield, was attained according to the results presented for IAP2B. A second goal was to maintain genetic variability for the trait under selection. Genotypic variance for grain yield was estimated to have increased significantly among S_1 families from C0 to C4 (in accordance with confidence intervals at $1 - \alpha = 0.90$) (Table 10). The increase for estimated genotypic variance in C4 may have been caused by linkage disequilibrium in the base population. The base population was initiated by crossing ten elite inbred lines (used as male parents) onto genetically male-sterile plants of an existing random-mating population. Equal portions of seed representing crosses with the ten inbreds were composited to form the base population (C0). Sixty S_1 families were chosen randomly from that population and evaluated along with 60 S_1 families from C4 in Experiment II. The C0 population was not intermated before the S_1 families were selected for my experiments.

Hanson (1959) suggested that a minimum of four parents and at least three to four generations of intermating should be used to synthesize a base population. By using that strategy, Hanson believed that a base population should approach linkage equilibrium. Without intermating, it is highly unlikely that my base population was in linkage equilibrium. As recurrent selection progressed over cycles, intermating of selected parents was practiced. With each random-mating, new genetic combinations were possible. The breakup of linkage blocks during these intermatings may have released hidden genetic variability that would account for the increased genotypic variance for grain yield estimated for C4.

Compositing of seed from 300 randomly pollinated plants was practiced

during each cycle, ensuring very large effective population sizes. Rawlings (1970) suggested that, if linkage effects are a concern, effective population size should be increased to allow for linkage depression. Large losses of positive genetic variability during the cycles of population advancement of IAP2B due to drift or the effects of selection seem unlikely. Hanson (1959) stated, "Selection for a simply inherited characteristic should be avoided in the intermating population because selection for specific types would tend to fix chromosome segments in the intermating population and thereby reduce the frequency of effective recombinations." Except for grain yield, the only conscious selection practiced in IAP2B was against extreme plant height and late maturity. Latter (1965, 1966a,b) stated that the effects of linkage on reduction of total response to selection were minor unless recombination probability among loci was less than 0.01.

The estimated increase of genotypic variance for grain yield in C4 may also have been modified due to changes in gene frequencies over successive cycles of selection. When genotypic variance is entirely a reflection of additive gene action, it is greatest when gene frequencies of favorable alleles are 0.5. When the degree of dominance is complete, maximum genotypic variance is attained when the frequency of the recessive allele is 0.71 (Falconer, 1981). If the frequency of favorable alleles was low in the base population, subsequent increases in gene frequency could have been responsible for moderately increased estimates of genotypic variance components for grain yield in C4.

Graphical representation of the phenotypic variability for grain

yield can be seen in Figure 1. The frequency distributions for C0 and C4 portray an effective accomplishment of the objectives of recurrent selection. The mean has shifted favorably and the range of phenotypes has been extended. The low S_1 family value has been increased from C0 to C4 (from 4.51 to 4.89) and so has the high S_1 family value (from 6.08 to 6.66) (Table 9). Mass selection for individual-panicle grain weight has been successful over four cycles for increasing grain yield.

Estimates of genotypic variance also increased for days to midbloom from C0 to C4 (Table 10). Again linkage disequilibrium in the base population, followed by intermatings in successive cycles of recurrent selection, may have accounted for the increased variability. Seeds/panicle, 100-seed weight, panicles/plant, and plant height did not exhibit significant differences (beyond $p < 0.10$) between C0 and C4 for genotypic variance.

Direct estimates of dominance variance were not determined by using data from my experiments. In theory, the genotypic variance estimated from evaluations of S_1 families represents all of the additive variance and one-fourth of the dominance variance sampled from the reference population. Evaluations of half-sib families reflect one-fourth of the additive variance. That premise is based on the following assumptions: (1) the population is random mating and there is adequate sampling of randomly chosen genotypes, (2) normal diploid inheritance, (3) no multiple alleles, (4) linkage equilibrium in the reference population, (5) no environmental correlation with genotypes, (6) no maternal effects, and (7) no epistasis (Hallauer and Miranda, 1988).

Adhering to theoretical expectations, the ratio $4\sigma^2HS:\sigma^2S_1$ should yield results that range < 1:1. Empirical results have produced variable estimates for the ratio (>1:1) in previous studies with sorghum (Jan-orn et al., 1976; Lothrup et al., 1985a). Jan-orn et al. (1976) listed two possible explanations for the large values estimated for $4\sigma^2HS$ when compared to σ^2S_1: (1) σ^2S_1 was less than $4\sigma^2HS$ when frequencies of favorable alleles were less than 0.5 and dominance variance and/or epistasis were important, and (2) $4\sigma^2HS$ was overestimated due to assortative mating in NP3R population. Lothrup et al. (1985a) believed there was an overestimation of $4\sigma^2HS$ and an underestimation of σ^2S_1 because of misclassification of male-fertile and male-sterile panicles in the isolation plantings of IAP1R(M) during anthesis. The authors of both experiments agreed that σ^2S_1 tended to be underestimated.

The effects of nonadditive gene action were estimated indirectly in Experiment I by determining the inbreeding depression from S0 to $S\infty$ (100% homozygosity). Population means for quantitatively inherited traits may show appreciabale change with inbreeding. Large values for inbreeding depression indicate that a large proportion of nonadditive gene action is being expressed for the trait under consideration because the heterozygote has a greater value than the homozygote.

Inbreeding depression for grain yield in IAP2B was estimated at -18.2% (Table 7). Lothrup et al. (1985a) and Kwolek et al. (1986) reported -13.6% and -29.6% inbreeding depression for grain yield in IAP1R and IAP3BR, respectively. Appreciable nonadditive genetic variance appears to be manifested in these random-mating sorghum populations.

The results of these studies are consistent with others that have examined genotypic variance components in sorghum populations. Jan-orn et al. (1976) reported that the ratio of dominance variance to additive variance for grain yield was 1.38:1 in NP3R. Bittenger et al. (1981) found that ratio to be 1.24:1 in PP9.

Nonadditive gene action plays a smaller role in the expression of other agronomic traits in sorghum. In IAP2B, estimates of inbreeding depression were -13.7% for panicles/plant, -11.5% for plant height, and -8.4% for 100-seed weight. Seeds/panicle and days to midbloom displayed additive gene action. Lothrup et al. (1985a) found inbreeding depression of -6.3% for seeds/panicle and -4.9% for 100-seed weight, but he reported that additive gene action was responsible for the expression of panicles/plant. Kwolek et al. (1986) did not observe significance (beyond $p < 0.05$) for nonadditive gene action in agronomic traits other than grain yield. Bittenger et al. (1981) reported that additive genetic variance was greater than dominance variance for eight traits (not including grain yield). Jan-orn et al. (1976) reported that dominance variance was important for seeds/panicle and grain yield, but not for other traits evaluated.

Heritability estimates for agronomic traits are important parameters for plant breeders to use in assessing the breeding potential of a population. Evaluation of a genotype by its phenotype is most efficient when nongenetic influences are minimized. Broad-sense heritability estimates relate the proportion of genotypic variability to total phenotypic variability. Heritability estimates from my experiments were

based on S_1 progeny means. If epistasis and dominance variance components are disregarded, the estimates reflect narrow-sense heritability. However, the inbreeding depression values determined in Experiment I suggest that nonadditive genetic variance plays a substantial role in the phenotypic expression for grain yield, and to a lesser degree, for other traits measured for IAP2B. By using heritability estimated from S_1 families, overestimation of narrow-sense heritability would result when nonadditive gene action was present.

The heritability estimate for grain yield among S_1 families of IAP2B increased significantly ($p < 0.10$) from C0 to C4 (Table 10). The higher proportion of genotypic variance in C4 compared to C0 was largely responsible for the increase from H = 0.68 in C0 to H = 0.78 in C4. Kwolek et al. (1986) also reported increased progeny-mean heritability for grain yield among S_1 families of IAP3BR population from C0 (0.58) to C4 (0.77). Similar estimates have been reported for the heritability of grain yield on a progeny-mean basis of 0.74 for IAP1R (Lothrup et al., 1985a), 0.71 for NP3R (Jan-orn et al., 1976), and 0.74 to 0.87 for NP3R, NP5R, and NP7BR (Eckebil et al., 1977).

A significant ($1 - \alpha = 0.90$) change in heritability from H = 0.85 in C0 to H = 0.74 in C4 was observed for panicles/plant in IAP2B. The decreased heritability parallels and reflects the decrease found for the genotypic variance for panicles/plant. The loss of genotypic variability may be a consequence of the procedure used during population advancement by gridded mass selection. The selection units were individual panicles within each grid that had the heaviest grain weights. That

selection criterion did not take into consideration the yield potential of tillers present. Thus, selection of plants that had a large main panicle may have indirectly selected against high-yielding genotypes with smaller main panicles but numerous tillers that contributed substantially to overall grain yield per unit area.

Although a reduction from C0 to C4 was shown for the heritability of panicles/plant, the estimate of 0.74 is still moderately high. The estimates for panicles/plant from my research were similar or slightly larger than those reported from other experiments conducted with random-mating sorghum populations. Lothrup et al. (1985a) examined S_1 and half-sib families from IAP1R in two experiments and found that heritability of panicles/plant on a progeny-mean basis ranged from 0.63 to 0.77. Ess and Atkins (1989) reported heritabilities of 0.40 and 0.57 for hybrids that involved male parents from IAP1R and IAP4R, respectively. Heritability on a progeny-mean basis for panicles/plant also was reported by Jan-orn et al. (1976) for S_1 families from NP3R (0.59) and by Eckebil et al. (1977) for NP3R, NP5R, and NP7BR (from 0.47 to 0.61).

Heritability estimated for other traits among S_1 families of IAP2B remained stable from C0 to C4. Plant height had the highest values (0.91 for both cycles), and heritability for days to midbloom (0.84 for C0, 0.89 for C4), seeds/panicle (0.82 for C0, 0.79 for C4), and 100-seed weight (0.85 for C0, 0.86 for C4) also were large. These estimates generally are in harmony with those reported from other studies with sorghum (Jan-orn et al., 1976; Eckebil et al., 1977; Lothrup et al., 1985a; Kwolek et al., 1986; Ess and Atkins, 1989).

Estimates of expected gain from selection offer plant breeders another indication of the breeding potential of a population. By using

estimates of variance components, progeny-mean heritability values, cycle means, and a 10% selection intensity, expected gains from S_1 family selection were determined from the C0 and C4 data in Experiment II (Table 11). Expressed as percentage gain relative to the cycle mean, expected response to S_1 family selection for grain yield was 2.0% per year for the C0 data and it increased to 3.2% per year for the C4. The larger response from selection for the C4 data was largely attributable to the increased genotypic variance estimated for that cycle.

Selection for individual-panicle grain weight in IAP2B has been effective for increasing grain yield over four cycles. Differences among genotypic and phenotypic correlations from C0 to C4 indicated that selection for individual-panicle grain weight also influenced some of the other characters measured (Table 12). Grain yield displayed little genotypic correlation (r_g = 0.08) with seeds/panicle in C0, but in C4 a moderately high correlation (r_g = 0.53) existed between these traits. Four cycles of selection for increased grain weight of individual panicles also increased the phenotypic correlation of grain yield with number of seeds/panicle to r_{ph} = 0.49. Investigations with other random-mating sorghum populations generally have shown that seeds/panicle and seeds/plant were the components most highly correlated with grain yield (Ess and Atkins, 1989; Lothrup et al., 1985b; Jan-orn et al., 1976).

Grain yield and panicles/plant were not correlated significantly (beyond $p < 0.05$) in C0, but they were correlated ($p < 0.05$) in C4 (r_{ph} = 0.38). Grain yield and 100-seed weight showed little genotypic

correlation in either C0 (r_g = 0.28) or C4 (r_g = -0.15), but the difference between cycles (0.43) is sizeable.

Stability of grain yield over different environments often results from interactions among the components of yield. Reductions or gains in some yield components generally involve an inverse relationship among other components (Kwolek, 1986). Strong negative genotypic correlations were observed between seeds/panicle and 100-seed weight in both C0 and C4 (-0.54 and -0.64, respectively). These coefficients are in harmony with those reported by Ess and Atkins (1989), Kwolek et al. (1986), Lothrup et al. (1985b), and Jan-orn et al. (1976). The values reflect compensatory effects among these yield components relative to their individual relationships with grain yield.

Genotypic and phenotypic correlations remained stable from C0 to C4 for grain yield with plant height, and also for grain yield with days to midbloom. Genotypic correlations for grain yield with plant height were small in both cycles (r_g = 0.12 and 0.13 for C0 and C4, respectively), but genotypic correlations were moderately strong for grain yield with days to midbloom in C0 and C4 (r_g = 0.55 and 0.50, respectively).

Expected correlated response values for unselected traits (Table 13) when selection among S_1 families was for grain yield, components of yield, days to midbloom, and plant height indicated that improvement of the traits by indirect selection generally would not be successful. In theory, the effectiveness of indirect selection requires that the trait selected should have a higher heritability than the trait of interest, and the selected trait should be highly correlated with the unselected

trait. Most genetic correlations among agronomic traits for IAP2B were not strong enough to facilitate effective use of indirect selection. Significant improvement in grain yield through selection for the other traits generally seemed unlikely, based on either the C0 or C4 data. It seems noteworthy, however, that selection of S_1 families for seeds/panicle, based on the C4 data, would be expected to produce an improvement in grain yield that would be almost 50% of that expected if selection were for grain yield itself. But, based on the C0 data, selection for seeds/panicle would have resulted in an expected loss of 9% for grain yield. If the trend toward a higher correlation between grain yield and seeds/panicle (Table 12) should persist through subsequent cycles, selection of S_1 families with high seeds/panicle could be an effective strategy for increasing grain yield.

SUMMARY

Genotypes selected from the random-mating sorghum population IAP2B(M) were evaluated in two experiments. Entries in Experiment I consisted of seed composites from pollen-fertile panicles (S_1 families) of C0, C2, C3, and C4, and from pollen-sterile panicles (half-sib families) of C1, C2, C3, and C4. In Experiment II, 120 S_1 families, 60 families chosen randomly from the base population (C0) and the fourth cycle (C4) were evaluated. The experiments were conducted to characterize and evaluate the breeding potential of IAP2B population *per se*, and to examine changes that occurred in plant characters from the initial through the fourth cycle of gridded mass selection for individual-panicle grain weight.

The genotypes in both experiments were evaluated by using replicated tests at Ames, Iowa during 1984 through 1988. Grain yield, seeds/panicle, 100-seed weight, and panicles/plant were evaluated in all five years in both experiments. Plant height data were taken during 1986 through 1988 for both experiments, and number of days to midbloom was recorded in 1987 and 1988 and 1986 through 1988 for Experiments I and II, respectively.

Results from both experiments indicated that gridded mass selection for individual-panicle grain weight was successful over four cycles for increasing grain yield. The mean for grain yield was shifted favorably, and the range among yields of S_1 families was extended. In Experiment I, grain yield of composites of S_1 families increased from 5.25 Mg/ha in C0 to 5.52 Mg/ha in C4, and in Experiment II, mean grain yield of S_1 families

increased from 5.41 Mg/ha in C0 to 5.66 Mg/ha in C4. Regression analyses in Experiment I did not distinguish a specific type of response in association with the increased grain yield observed among composites of S_1 or half-sib families. In Experiment II, the low S_1 family value increased from C0 to C4 (from 4.51 to 4.89 Mg/ha) and so did the high S_1 family value (from 6.08 to 6.66 Mg/ha). Four cycles of gridded mass selection for individual-panicle grain weight also increased seeds/panicle, 100-seed weight, days to midbloom, and plant height, but it decreased panicles/plant.

Estimates of genotypic variance among S_1 families in Experiment II increased from C0 to C4 for grain yield and days to midbloom, but the estimates did not change for the other traits (in accordance with confidence intervals at $1 - \alpha = 0.90$). Linkage disequilibrium in the base population followed by recombination of selected parents in subsequent cycles of population advancement were likely reasons for the increased genotypic variance observed for grain yield and days to midbloom in C4.

The effects of nonadditive gene action were estimated indirectly in Experiment I by estimating inbreeding depression percentages for S0 to $S\infty$ (100% homozygosity). The estimates were -18.2% for grain yield, -13.7% for panicles/plant, -11.5% for plant height, and -8.4% for 100-seed weight, indicating that appreciable nonadditive gene action was expressed for these traits. Seeds/panicle and days to midbloom displayed additive gene action.

Phenotypic and genotypic coefficients of correlation among characters were similar in magnitude. Differences among the correlations

in C0 and C4 indicated that selection for individual-panicle grain weight also influenced some of the other characters measured. Coefficients of correlation changed substantially in a positive direction from C0 to C4 for grain yield vs seeds/panicle, grain yield vs panicles/plant, and seeds/panicle vs panicles/plant, but they changed in a negative manner for grain yield vs 100-seed weight. The positive correlations between grain yield and days to midbloom, 100-seed weight and plant height, and panicles/plant with plant height were of similar magnitude in C0 and C4, as were the negative correlations between seeds/panicle and 100-seed weight and seeds/panicle with plant height.

Heritability estimates on a progeny-mean basis generally were high for the traits evaluated in Experiment II. Grain yield for S_1 families in C0 had the lowest value ($H = 0.68$) and plant height for the C0 families was highest ($H = 0.91$). Heritability estimates increased for grain yield from C0 to C4, but they decreased for panicles/plant (in accordance with confidence intervals at $1 - \alpha = 0.90$). Estimates of heritability were similar in C0 and C4 for the other characters.

Expected gain/year for grain yield by using S_1 family selection with replicated yield trials increased from 2.0% of the mean, based on C0 data, to 3.2% based on the C4 data. In contrast, the estimates for C0 vs C4 showed a decrease for panicles/plant (from 4.5% to 3.6% of the mean). Differences between C0 and C4 for expected gains were considerably smaller for the other traits.

Expected correlated response values for unselected traits indicated that indirect selection generally would not be successful for improvement

of grain yield, components of yield, days to midbloom, and plant height. Estimates from the C0 and C4 data indicated that selection for grain yield would reflect a moderate increase in days to midbloom. Response values for the S_1 families from C4 suggested that selection for yield also would produce moderate increases in seeds/panicle and panicles/plant. Genetic correlations among agronomic traits for IAP2B lacked the strength needed to facilitate effective use of indirect selection.

Genetic and agronomic parameters determined for the genotypes indicated that IAP2B(M) sorghum population should provide germplasm useful for developing female parents that possess a wide array of genes and gene combinations that are needed to diversify hybrid sorghum seed production. The higher estimates of genotypic variance and heritability for grain yield in C4, as well as larger estimates of expected gains from S_1 family selection, indicate that further improvement of the population should be expected with additional cycles of recurrent selection.

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APPENDIX

Table A1. Means, standard errors, least significant differences, and high and low S_1 family values for agronomic traits in Experiment II at Ames, Iowa during 1984

Trait and cycle of selection	Mean	LSD(0.05) C0 mean vs C4 mean	S_1 family values		LSD(0.05) among S_1 families
			Low	High	
Grain yield (Mg/ha)					
C0	5.73 ± 0.045		4.39	6.75	
C4	6.16 ± 0.056		5.00	7.16	
		0.14			1.09
Seeds/panicle					
C0	1987 ± 27		1485	2741	
C4	2130 ± 27		1484	2807	
		76			592
100-seed weight (g)					
C0	2.33 ± 0.024		1.72	3.02	
C4	2.37 ± 0.022		1.84	2.92	
		0.07			0.50
Panicles/plant					
C0	1.37 ± 0.014		0.98	1.81	
C4	1.35 ± 0.015		1.04	1.69	
		0.04			0.33

Table A2. Means, standard errors, least significant differences, and high and low S_1 family values for agronomic traits in Experiment II at Ames, Iowa during 1985

Trait and cycle of selection	Mean	LSD(0.05) C0 mean vs C4 mean	S_1 family values		LSD(0.05) among S_1 families
			Low	High	
Grain yield (Mg/ha)					
C0	4.36 ± 0.023		3.64	5.14	
C4	4.54 ± 0.024		3.71	5.30	
		0.07			0.52
Seeds/panicle					
C0	1576 ± 17		1208	2172	
C4	1709 ± 14		1269	2406	
		43			333
100-seed weight (g)					
C0	2.33 ± 0.022		1.74	3.05	
C4	2.30 ± 0.017		1.56	3.03	
		0.06			0.42
Panicles/plant					
C0	1.28 ± 0.010		1.05	1.57	
C4	1.25 ± 0.008		1.04	1.50	
		0.03			0.19

Table A3. Means, standard errors, least significant differences, and high and low S_1 family values for agronomic traits in Experiment II at Ames, Iowa during 1986

Trait and cycle of selection	Mean	LSD(0.05) C0 mean vs C4 mean	S_1 family values		LSD(0.05) among S_1 families
			Low	High	
Grain yield (Mg/ha)					
C0	6.14 ± 0.030		5.60	6.79	
C4	6.26 ± 0.028		4.89	6.88	
		0.08			0.65
Seeds/panicle					
C0	1389 ± 18		952	2072	
C4	1386 ± 17		925	1764	
		49			381
100-seed weight (g)					
C0	2.91 ± 0.023		2.09	3.56	
C4	3.00 ± 0.020		2.16	3.68	
		0.06			0.47
Panicles/plant					
C0	1.74 ± 0.021		1.29	2.46	
C4	1.72 + 0.020		1.13	3.08	
		0.06			0.44
Days to midbloom					
C0	69.7 ± 0.09		66.5	73.0	
C4	70.6 ± 0.01		66.5	73.5	
		0.3			2.0
Plant height (cm)					
C0	115 ± 0.63		98	141	
C4	124 ± 0.66		109	146	
		2			14

Table A4. Means, standard errors, least significant differences, and high and low S_1 family values for agronomic traits in Experiment II at Ames, Iowa during 1987

Trait and cycle of selection	Mean	LSD(0.05) C0 mean vs C4 mean	S_1 family values		LSD(0.05) among S_1 families
			Low	High	
Grain yield (Mg/ha)					
C0	4.94 ± 0.042		3.25	5.97	
C4	5.07 ± 0.040		3.87	6.78	
		0.11			0.88
Seeds/panicle					
C0	1433 ± 21		975	1997	
C4	1390 ± 19		771	2012	
		56			430
100-seed weight (g)					
C0	2.38 ± 0.025		1.86	2.88	
C4	2.53 ± 0.018		1.91	3.49	
		0.06			0.48
Panicles/plant					
C0	1.65 ± 0.014		1.25	2.05	
C4	1.64 ± 0.016		1.20	2.25	
		0.04			0.32
Days to midbloom					
C0	66.1 ± 0.08		63.5	70.0	
C4	67.4 ± 0.08		64.0	70.5	
		0.2			1.7
Plant height (cm)					
C0	112 ± 0.49		89	145	
C4	121 ± 0.62		99	158	
		2			12

Table A5. Means, standard errors, least significant differences, and high and low S_1 family values for agronomic traits in Experiment II at Ames, Iowa during 1988

Trait and cycle of selection	Mean	LSD(0.05) C0 mean vs C4 mean	S_1 family values		LSD(0.05) among S_1 families
			Low	High	
Grain yield (Mg/ha)					
C0	5.87 ± 0.044		4.62	7.01	
C4	6.26 ± 0.045		4.90	7.90	
		0.12			0.95
Seeds/panicle					
C0	1785 ± 24		1301	2181	
C4	1779 ± 20		1222	2396	
		62			478
100-seed weight (g)					
C0	2.28 ± 0.030		1.77	2.87	
C4	2.51 ± 0.024		1.79	3.07	
		0.08			0.58
Panicles/plant					
C0	1.62 ± 0.015		1.34	2.30	
C4	1.59 ± 0.013		1.25	1.98	
		0.04			0.30
Days to midbloom					
C0	65.5 ± 0.11		61.5	71.0	
C4	67.9 ± 0.13		62.5	74.5	
		0.3			2.6
Plant height (cm)					
C0	112 ± 0.51		97	145	
C4	120 ± 0.63		99	157	
		2			12

Table A6. Mean squares from the analyses of variance for grain yield and the components of yield for Experiment II at Ames, Iowa in 1984

Source of variation	df	Grain yield ($x10^{-1}$)	Seeds/ panicle ($x10^{4}$)	100-seed weight ($x10^{-2}$)	Panicles/ plant (10^{-2})
Sets (S)	5	1.67	77.56	27.71	2.94
Replications/S	6	5.91	3.64	7.42	6.24
Genotypes (G)/S	114	6.29**	14.29**	17.91**	4.37**
C0/S	54	5.10**	12.30*	18.97**	5.13**
C4/S	54	5.71	15.11	16.98**	3.77
C0 vs C4/S	6	22.21**	24.90	16.85	2.86
Error	114	3.03	8.94	6.38	2.84
C0/S/R	54	2.43	8.89	7.01	2.44
C4/S/R	54	3.70	8.46	5.82	2.71
C0 vs C4/S/R	6	2.37	13.76	5.84	7.61
CV (%)		9.26	14.53	10.73	12.41

Table A7. Mean squares from the analyses of variance for grain yield and the components of yield for Experiment II at Ames, Iowa in 1985

Source of variation	df	Grain yield ($x10^{-1}$)	Seeds/ panicle ($x10^{4}$)	100-seed weight ($x10^{-2}$)	Panicles/ plant ($x10^{-2}$)
Sets (S)	5	9.90	4.06	37.50	2.46
Replications/S	6	4.09	3.39	7.70	0.82
Genotypes (G)/S	114	2.52**	10.73**	19.30**	2.83**
C0/S	54	1.82**	7.35**	20.03**	2.95**
C4/S	54	3.02**	11.68**	17.62**	2.65**
C0 vs C4/S	6	4.41	32.63**	27.89**	3.37*
Error	114	0.68	2.84	4.56	0.95
C0/S/R	54	0.65	3.48	5.87	1.18
C4/S/R	54	0.68	2.32	3.39	0.77
C0 vs C4/S/R	6	1.06	1.67	3.30	0.50
CV (%)		5.87	10.25	9.23	7.72

Table A8. Mean squares from the analyses of variance for grain yield, the components of yield, days to midbloom and plant height for Experiment II at Ames, Iowa in 1986

Source of variation	df	Grain yield ($x10^{-1}$)	Seeds/ panicle (10^4)	100-seed weight ($x10^{-2}$)	Panicles/ plant ($x10^{-2}$)	Days to midbloom	Plant height ($x10^1$)
Sets (S)	5	3.44	17.81	14.26	40.49	1.63	12.85
Replications/S	6	1.92	7.36	3.92	10.13	2.58	17.45
Genotypes (G)/S	114	2.01**	9.09**	21.62**	14.11**	5.78**	23.86**
C0/S	54	1.43	8.65**	20.62**	11.79**	4.23**	19.28**
C4/S	54	2.54**	8.27**	19.51**	15.27**	6.76**	21.96**
C0 vs C4/S	6	2.40	20.46**	49.70**	24.59**	10.96*	82.14**
Error	114	1.06	3.70	5.53	4.84	1.04	5.02
C0/S/R	54	1.05	3.93	6.29	5.20	1.19	4.71
C4/S/R	54	0.97	3.66	4.77	4.73	0.73	5.15
C0 vs C4/S/R	6	2.09	2.02	5.58	2.55	2.43	6.67
CV (%)		5.26	13.87	7.96	12.72	1.45	5.93

Table A9. Mean squares from the analyses of variance for grain yield, the components of yield, days to midbloom and plant height for Experiment II at Ames, Iowa in 1987

Source of variation	df	Grain yield ($x10^{-1}$)	Seeds/ panicle ($x10^{4}$)	100-seed weight ($x10^{-2}$)	Panicles/ plant ($x10^{-2}$)	Days to midbloom	Plant height ($x10^{1}$)
Sets (S)	5	12.21	19.71	7.66	11.05	6.69	34.58
Replications/S	6	0.73	7.67	4.57	17.67	4.55	5.13
Genotypes (G)/S	114	3.63**	14.10**	15.14**	7.33**	6.36**	31.67**
C0/S	54	4.59**	12.82**	12.27*	6.86**	5.04**	24.89**
C4/S	54	7.73**	14.57**	15.57**	7.11**	6.39**	30.28**
C0 vs C4/S	6	5.53	21.38*	37.26*	13.51*	17.82**	105.29**
Error	114	1.98	4.72	5.78	2.62	0.73	3.73
C0/S/R	54	2.12	5.34	7.56	2.26	0.68	2.91
C4/S/R	54	1.88	4.18	3.92	3.00	0.81	4.67
C0 vs C4/S/R	6	1.60	4.03	6.45	2.33	0.52	2.66
CV (%)		8.89	15.39	9.79	9.85	1.28	5.26

Tabla A10. Mean squares from the analyses of variance for grain yield, the components of yield, days to midbloom and plant height for Experiment II at Ames, Iowa in 1988

Source of variation	df	Grain yield ($x10^{-1}$)	Seeds/ panicle ($x10^{4}$)	100-seed weight ($x10^{-2}$)	Panicles/ plant ($x10^{-2}$	Days to midbloom	Plant height ($x10^{1}$)
Sets (S)	5	13.33	11.58	0.88	30.87	2.04	37.91
Replications/S	6	16.11	13.16	12.35	5.06	4.65	31.18
Genotypes (G)/S	114	8.55**	11.23**	18.66**	4.11**	18.17**	26.68**
C0/S	54	5.47**	10.74*	15.87	4.36	12.22**	17.16**
C4/S	54	10.41**	12.03**	15.30**	3.66**	18.55**	27.75**
C0 vs C4/S	6	19.50**	8.45	74.02**	5.80	68.30**	102.71**
Error	114	2.31	5.83	8.68	2.32	1.72	3.55
C0/S/R	54	2.37	6.80	10.77	2.82	1.48	3.11
C4/S/R	54	2.42	5.03	6.83	1.89	2.06	4.74
C0 vs C4/S/R	6	0.87	4.31	6.49	1.79	0.94	2.89
CV (%)		7.92	13.55	12.30	9.48	1.97	5.13